NOV 21 1919

JOURNAL OF ANATOMY

ORIGINALLY THE JOURNAL OF ANATOMY AND PHYSIOLOGY

CONDUCTED ON BEHALF OF THE ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND BY

PROFESSOR THOMAS H. BRYCE — UNIVERSITY OF GLASGOW
PROFESSOR EDWARD FAWCETT — UNIVERSITY OF BRISTOL
PROFESSOR J. P. HILL — UNIVERSITY OF LONDON
PROFESSOR G. ELLIOT SMITH — UNIVERSITY OF MANCHESTER
PROFESSOR ARTHUR KEITH — ROYAL COLLEGE OF SURGEONS

LINCOLN'S-INN-FIELDS, LONDON, W.C. 2

VOLUME LIII

PART IV

JULY 1919

Entered at New York Post Office as Second Class Matter

(All Rights reserved)

CAMBRIDGE UNIVERSITY PRESS
C. F. CLAY, MANAGER
LONDON: FETTER LANE, E.C. 4

also

H. K. LEWIS & CO., LTD., 136, GOWER STREET, LONDON, W.C. 1
WILLIAM WESLEY AND SON, 28, ESSEX STREET, LONDON, W.C. 2
CHICAGO: THE UNIVERSITY OF CHICAGO PRESS
BOMBAY, CALCUTTA, MADRAS: MACMILLAN & CO., LTD.
TORONTO: J. M. DENT & SONS, LTD.
TOKYO: THE MARUZEN-KABUSHIKI-KAISHA

Price Seven shillings and Sixpence net

...O CAMB...
Microsco...

...GE.
...ves, and
...for these
...ed by those
...ers in
...ill, sold or ex-
...AMBRIDGE.

BIOMETRIKA

A JOURNAL FOR THE STATISTICAL STUDY OF BIOLOGICAL ...S

FOUNDED BY

W. F. R. WELDON, FRANCIS GALTON AND ...

EDITED BY

KARL PEARSON

Vol. XII, Parts I & II *November* ... 1918

CONTENTS

I. On the Standard Deviations of Correlated and Uncorrelated *Functions* and the Constants of the Curves of Distribution of Observational Errors. By KARL PEARSON, ...

II. On the Product-Moments of Various Orders of the Normal Frequency Variable. By K. PEARSON and A. ...

III. The Correlation Coefficient of a Polychoric ...

IV. On a Formula for the Product-Moment Coefficient ... Normal Frequency Distribution in any Number of Variables. By ...

V. On the Mathematical Expectation of the Moments ... AL. A. TCHOUPROFF of Petrograd. PART I ...

MISCELLANEA:

(i) Preliminary Note on the Application of ... Capacity. By M. L. TIL...

(ii) Sur les moments de la fonction de corrélation. ... BASSETKOM, Stockholm ...

(iii) Formulae for determining the Mean Values of ... Coefficients in terms of the Variables in ... L. FARRELL, D.Sc. ...

Cambridge University Press, ...
C. F. CLAY, Manager ...

A PRELIMINARY NOTE ON THE MORPHOLOGY OF THE CORPUS STRIATUM AND THE ORIGIN OF THE NEOPALLIUM

By G. ELLIOT SMITH, F.R.S.

If a transverse section be made through the cerebral hemisphere of the archaic reptile *tuatara* (*Sphenodon*) a short distance in front of the lamina terminalis an arrangement such as I have represented in the diagram (fig. 1)

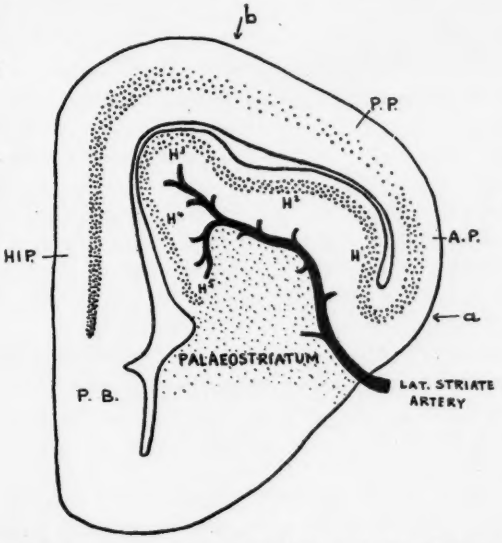


Fig. 1. Diagram of a transverse section of the right cerebral hemisphere of *Sphenodon*.

will be revealed. The ventral parts of the hemisphere consist of solid masses of grey matter forming the paraterminal body (*P.B.*) and the basal nucleus of the lowlier vertebrates, for which I shall adopt Ariëns Kappers's term "palaeostriatum." The rest of the section consists of pallium containing a column of cortical cells, every part of which is in unbroken continuity with the rest. In the inner wall the cells of the cortical column (*HIP.*) are densely packed to form the hippocampal formation, as yet undifferentiated into a definite fascia dentata and hippocampus sensu stricto. In the roof of the hemisphere the cells become more loosely packed (at the point marked *b*), and the hippocampus passes without any such sudden break (such as is seen

in the Lacertilia, Ophidia and Mammalia) into the parahippocampal pallium (*P.P.*), which is the homologue of what in mammals is sometimes called subiculum hippocampi. But this much abused term is employed so loosely and with such a variety of meanings that it would introduce unnecessary confusion to use it here. The parahippocampal pallium is the area beyond the limits of the true hippocampal formation (in Sauropsida and Mammalia) many of the fibres of which behave as hippocampal and not as neopallial elements, i.e. they pass into the fornix system and not into the internal capsule.

The parahippocampal pallium passes into the area pyriformis (*A.P.*), which is not strictly identical with the lobus pyriformis of the mammalian brain, but represents the pallial area which becomes further modified in mammals to develop into the true pyriform lobe. It is in fact a primordium lobi pyriformis.

At the point *a* the band of cortical cells suddenly bends inward toward the ventricle without any disturbance of the superficial layer of the pallium, which still remains in unbroken continuity with the surface of the palaeostriatum, without the intervention of any furrow. The ingrowing pallium extends around the upper part of the palaeostriatum forming an extensive cap (H^1, H^2, H^3, H^4 and H^5) which occupies the greater part of the cavity of the ventricle. As no term at present in use[1] can be applied to this remarkable appendage of the lateral pallium without serious ambiguity I shall refer to it at present as the "hypopallium." It is pallial in origin; it lies below the main portion of the pallium which forms the roof of the hemisphere; and, morphologically and functionally, it is analogous to but upon a lower plane of usefulness than the neopallium.

Along the boundary line between the palaeostriatum and the hypopallium there is found in certain sections a group of very large veins and an artery (*lat. striate artery*). When first (1897) I examined these sections (figs. 2 and 3) of the brain of *Sphenodon* and saw the large cleft (fig. 3, above the uppermost *P*) between the hypopallium and the palaeostriatum I imagined that originally there had been a deep fissure extending from the lateral surface (as far as H^5 in fig. 1) into which the great vessels had passed: and I assumed that the continuity of the tissues of the palaeostriatum and the hypopallium had been brought about by a secondary adhesion of their surfaces. Hence in the diagram[2] which I published in 1902 I represented a fissure in the place where the lateral striate artery is shown in fig. 1. After that diagram was drawn I studied the process of development of the hypopallium in a series of embryos of *Sphenodon*, kindly placed at my disposal by the late Professor G. B. Howes, F.R.S., and found that the column of cortical cells (H^1, H^2, H^3, H^4 and H^5)

[1] On a later page I shall explain the nature of the confusion involved in the use of the terms "epistriatum" and "neostriatum."

[2] Descriptive and Illustrated Catalogue of the Physiological Series of Comparative Anatomy contained in the Museum of the Royal College of Surgeons of England, vol. II. 2nd edition, 1902, fig. 33, p 123

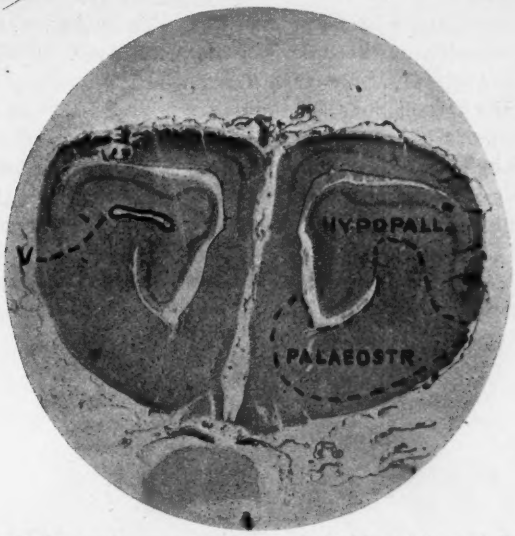


Fig. 2. Photograph of a transverse section of the cerebral hemispheres of *Sphenodon* stained (in 1897) with lithium carmine. The plane of the section passes a short distance in front of the optic chiasma. On the left side the course of the large artery and veins which proceed along the boundary line between the pallial structure or hypopallium and the palaeostriatum (the extent of which is indicated on the right side) is indicated by the broken line *V*.

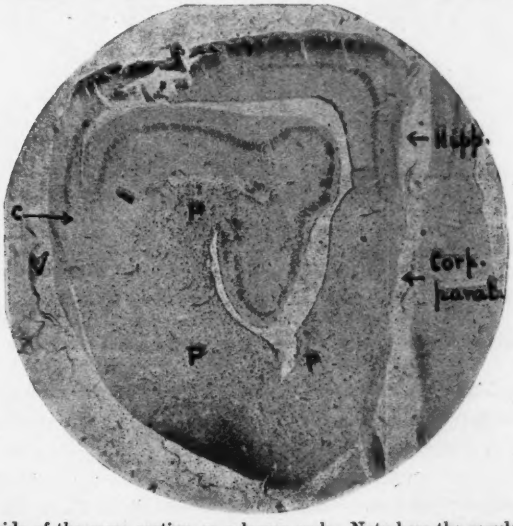


Fig. 3. The left side of the same section on a larger scale. Note how the regular and unbroken (except from damage to the section) column of cells, which extends from the inner wall (Hipp. = hippocampus) across the roof, suddenly bends inwards at *c.* to form the hypopallium, which forms a cap upon the palaeostriatum (*PPP.*). The paraterminal body (*Corp. parat.*) extends from the ventral margin of the hippocampal formation (*Hipp.*) to the part of the palaeostriatum that lies in the inner wall of the ventricle.

increased in width and buckled in towards the ventricle, without disturbing or in any way modifying the surface of the hemisphere. In other words, no fissure was formed; the large vessels made their way along the boundary line between the hypopallium and the palaeostriatum, but not in a fissure.

No notice was taken by any subsequent writer of my brief reference[1] to this remarkable arrangement of the pallium in *Sphenodon;* but when in my Arris and Gale Lectures at the Royal College of Surgeons in 1909 I referred to the structure which in this communication I call the "hypopallium" as a derivative of the cerebral cortex, my statements were subjected to adverse criticism by the Amsterdam and Frankfurt schools of investigators. But none of my critics seems to have realized that, when I referred to the hypo-

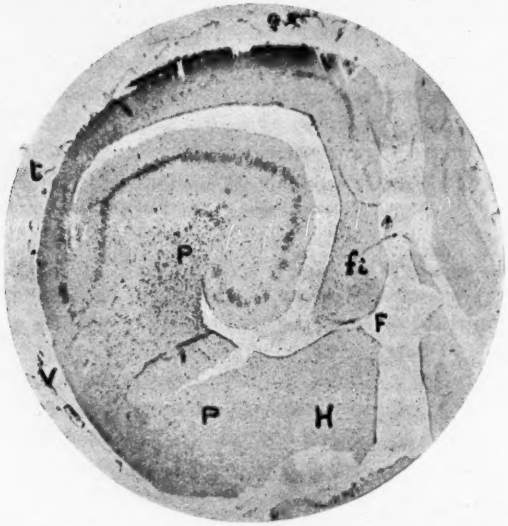


Fig. 4. A section (from the same series) passing through the foramen of Monro (*F.*). *H.* is the hypothalamus, which is in unbroken continuity with the palaeostriatum (*P.P.*), which projects upward to form a high crest around which the hypopallium with its regular layer of cortical cells is folded. *V.* is the boundary (upon the surface) between the hypopallium and the palaeostriatum. *t.* is an area of thinning of the lateral pallium. *fi.* is the corpus fimbriae.

pallium of *Sphenodon* as cerebral cortex, I was not theorizing but stating a fact that must be obvious to everyone who examines the photographs reproduced in figs. 2, 3 and 4.

[1] In the Catalogue of the Royal College of Surgeons, *op. cit.* fig. 33, p. 123. In her inaugural dissertation for the doctorate of the University of Basle ("Das Gehirn von Hatteria punctata," 1907, p. 19) Julia Gisi refers to the arrangement of the pallium in *Sphenodon* (*Hatteria*) in these words: [the cortex] "setzt sich vielmehr lateralwärts fort biegt dann in die Striatumrinde ein." But she gives no indication of any realization of the novelty or importance of this observation or of the fact that I had referred to this striking feature in the brain of *Sphenodon* five years before her memoir was written.

When first in 1897 I made these observations upon the brain of *Sphenodon* I did not lay any great stress upon these peculiar arrangements of the cortex because I did not look upon my discovery as a novelty. For in the previous year Edinger had described the structure which he called "epistriatum" in the brains of Chelonia, Lacertilia and Ophidia; and I imagined that he intended to apply this term to what I call the hypopallium in this communication. As Edinger (in 1896) had described his "epistriatum" in the tortoise as "an intilting (Einstülpung) of the cerebral cortex, the constituent cells of which are indistinguishable from cortical cells[1]," I thought in 1897 that my observations upon the brain of *Sphenodon* had not revealed any new fact. At that time I did not appreciate the confusion Edinger had introduced by his

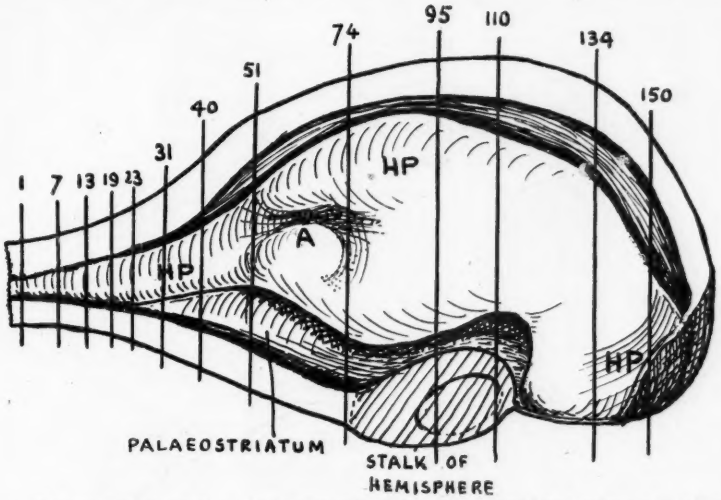


Fig. 5. The ventricular aspect of the lateral wall of the right cerebral hemisphere of *Sphenodon* exposed by removing the medial wall. *H.P.* is the hypopallial eminence. *A.* the longitudinal furrow on the hypopallium. The vertical lines and the numbers alongside them indicate the positions and distances between the series of sections shown in fig. 6.

failure to define his new term, which he employed in that memoir of 1896 in three or four different and incompatible senses[2]. Nor, of course, could I have foreseen that he and his school would in later years ignore the evidence of its continuity and structural conformity with the pallium and repudiate the view that the hypopallium was derived from the cerebral cortex.

The first point which I want to emphasize is that the whole of the hypopallial eminence, its extent not merely in the transverse plane (fig. 1, H^1 to H^5) but also in the longitudinal direction—from the extreme anterior end

[1] L. Edinger, "Neue Studien über das Vorderhirn der Reptilien," *Abhandlungen der Senckenberg. Naturforsch. Gesellschaft*, 1896, Bd. 19, p. 358. I shall explain later that Edinger was not really referring to the hypopallium but to the primordium neopallii.

[2] *Vide infra.*

to the postero-inferior recess of the hemisphere (fig. 5, *HP*)—is composed of pallium with a well-defined and unmistakable band of cortical cells (fig. 6). In figs. 7, 8, 9 and 10 careful drawings show the exact distribution of the cellular elements in four sections of the *Sphenodon* series, which I stained with lithium carmine in 1897.

Sphenodon is a survival of one of the most archaic types of reptile; and its brain represents with diagrammatic clearness the real constitution of the

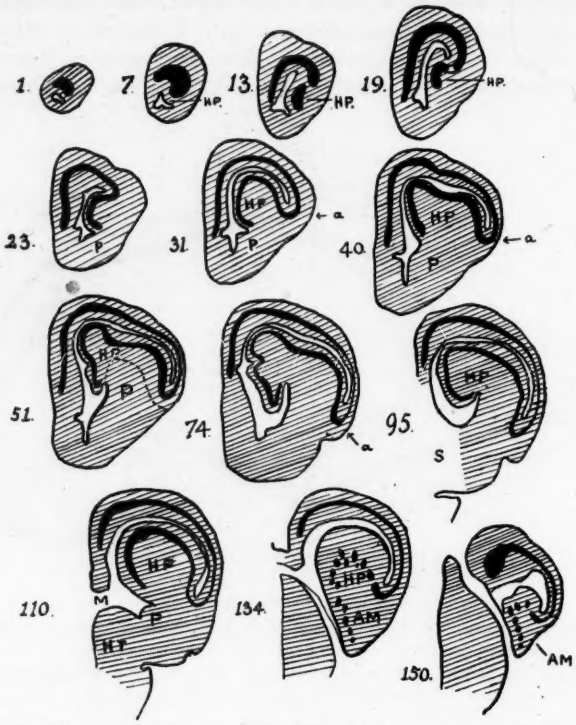


Fig. 6. Diagrams of a series of sections of the right cerebral hemisphere of *Sphenodon* cut in the planes shown in fig. 5. The band of cortical cells is shown as a solid black line which in the hypopallium of sections 134 and 150 becomes broken up into islands. *M.* foramen of Monro. *HP.* hypopallium. *P.* palaeostriatum. *HT.* hypothalamus. *AM.* amygdalar part of the hypopallium.

various parts of the reptilian hemisphere in a way that does not admit of any misunderstanding. But although the regular arrangement of the band of cortical cells is not preserved in the hypopallium of the other reptilian Orders, careful examination of *actual sections* (rather than the illustrations in memoirs) of Chelonian, Lacertilian and Ophidian brains clearly reveals substantially the same arrangement as is found in *Sphenodon*, except that the cortical band becomes broken up and its cells scattered in the hypopallium

of these other Orders. Even de Lange, on the very pages of his memoir[1], which are devoted to proclaiming that "the epistriatum is not cortical, but striatal," presents a drawing of a lizard's brain (reproduced here as fig. 11) which illustrates my contention. The hypopallium (the "epistriatum" of de Lange's memoir) is obviously an inward extension of the pallium. De Lange has not failed to notice this fact which so ill accords with his argument. He writes (pp. 787 and 788): "The large, ventricularly-directed part of the epistriatum has a cell-type which in form, staining-reactions and arrangement shows an affinity with the underlying palaeostriatal part of the brainwall.

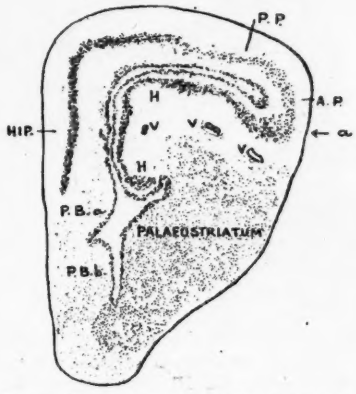


Fig. 7. Transverse section (27) of the right cerebral hemisphere of *Sphenodon* stained with lithium carmine. *HIP.* hippocampal formation. *P.P.* parahippocampal pallium. *A.P.* area pyriformis. *a.* place of inbending of the column of cortical cells. *H.H.* hypopallium. *V.V.V.* sections of large blood vessels (lateral striate arteries and veins). *P.B.a.* paraterminal body—fimbrial part. *P.B.b.* ventral part of paraterminal body.

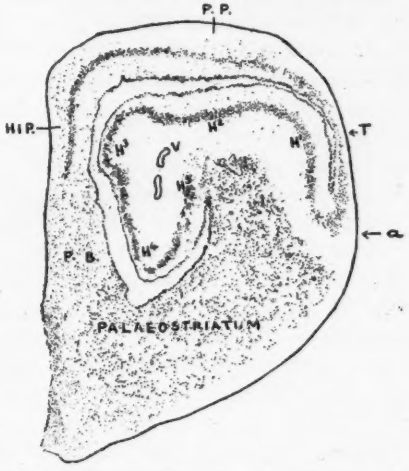


Fig. 8. Section 90 of the same series. Note how the cortical column, bending in at *a.*, passes right round (H^1, H^2, H^3, H^4 and H^5) the ventricular surface of the hypopallium to end upon the medial aspect of the dorsal crest of the palaeostriatum. *V.* large blood vessels. *T.* area of pallial thinning. *P.B.* paraterminal body. *P.P.* parahippocampal pallium.

However there is an extension into the dorsal layer of the epistriatum of cells which in their properties (form, staining and arrangement) reveal their affinities with the neighbouring plate of palaeocortex." In spite of this he claims that the "epistriatum is striatal not cortical." Elsewhere in his memoir (p. 590 *et seq.*) de Lange discriminates between the anterior and the posterior halves of the hypopallium in *Varanus*, calling the anterior part "neostriatum" and the posterior part "epistriatum." In fig. 12 is shown a sagittal section[2]

[1] S. J. de Lange, "Das Vorderhirn der Reptilien," *Folia Neuro-biologica*, Bd. v. 1911, pp. 587 and 588, fig. 43.

[2] I am indebted to Professor W. H. Wilson, of the Cairo School of Medicine, for the sections of this brain.

through the cerebral hemisphere of the common Egyptian *waran* (*Varanus griseus*) showing the hypopallium as a continuous band separated from the underlying palaeostriatum by a clear band (*c.c.*). It is important to note that the anterior end of the hypopallium passes into continuity with the primordium neopallii[1], a relationship which I shall discuss further in the following pages. To emphasize these points further I have reproduced a photograph (fig. 13) of a similar section through the hemisphere of a foetal lizard (*Lacerta viridis*).

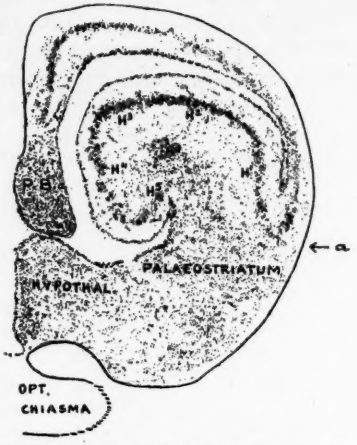


Fig. 9. Section 100 of the same series, passing through the foramen of Monro and the optic chiasma. H^1, H^2, H^3, H^4 and H^5, hypopallium.

In two figures representing sections through the brain of *Testudo graeca*[2] de Lange gives an admirable graphic demonstration of the fact that in the Chelonia essentially the same conditions prevail as I have described in *Sphenodon*. But the reality of this identity has recently been demonstrated beyond any possibility of error by J. B. Johnston[3]. In the former memoir he states that the hypopallium (which he calls "the dorsal ventricular ridge") "appears to be formed by an involution of the pallium": but he makes the remarkable qualification that "this ventricular ridge is a wholly different structure from the 'epistriatum' of Kappers" (p. 418). But the memoirs (to which I have already referred) written in Kappers's laboratory by de Lange indicate that the Chelonian "epistriatum" of Dutch writers seems to be what Johnston calls the "dorsal ventricular ridge." To avoid this fresh element of controversy I have avoided using Johnston's term and coined the new descriptive designation "hypopallium."

In the second of the two memoirs to which I have referred Johnston comes more definitely into line with the position I have taken during the last twenty years. Thus he says: "The cell layers of the general pallium turn in

[1] Although I have been using the term "primordium neopallii" in my note-books for the past nine years I have never hitherto employed it in print. In the meantime Elizabeth Caroline Crosby has independently invented the same term ("The Forebrain of Alligator Mississippiensis," *Journal of Comparative Neurology*, vol. XXVII. 1917, p. 395) and applied it in the same sense as I have used it in these notes. Hence any credit for a label which is necessary in describing the reptilian brain belongs to her.

[2] S. J. de Lange, "Das Zwischenhirn und das Mittelhirn der Reptilien," *Folia Neuro-biologica*, Bd. VII. 1913, pp. 104 and 105, figs. 30 and 31.

[3] "The cell masses in the forebrain of the turtle, Cistudo carolina," *Journal of Comparative Neurology*, vol. XXV. 1915, p. 393; also "The development of the dorsal ventricular ridge in turtles," *ibid.*, vol. XXVI. 1916, p. 481.

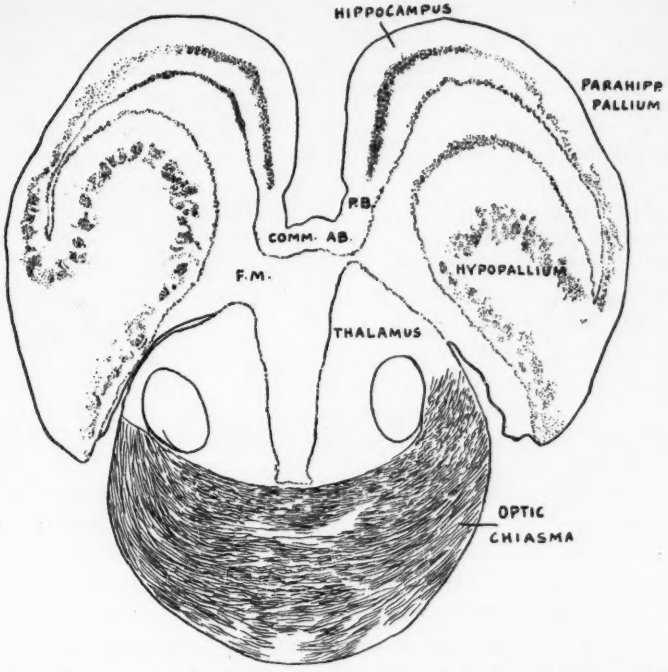


Fig. 10. Transverse section through the cerebrum of *Sphenodon* in the plane of the aberrant part of the hippocampal commissure (*Comm. ab.*). The continuity of the cortical layer of cells in the caudal (amygdalar) part of the hypopallium is displayed most clearly on the left side of this section.

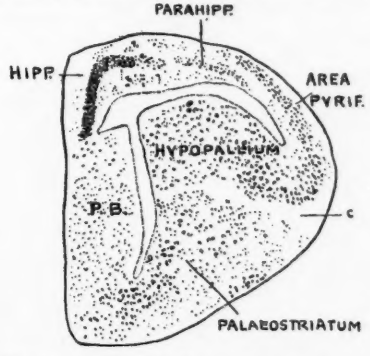


Fig. 11. De Lange's diagram of a transverse section through the brain of *Lacerta agilis* —the labels being those employed elsewhere in these notes (compare fig. 8). *c.* refers to the clear band separating the hypopallium from the palaeostriatum.

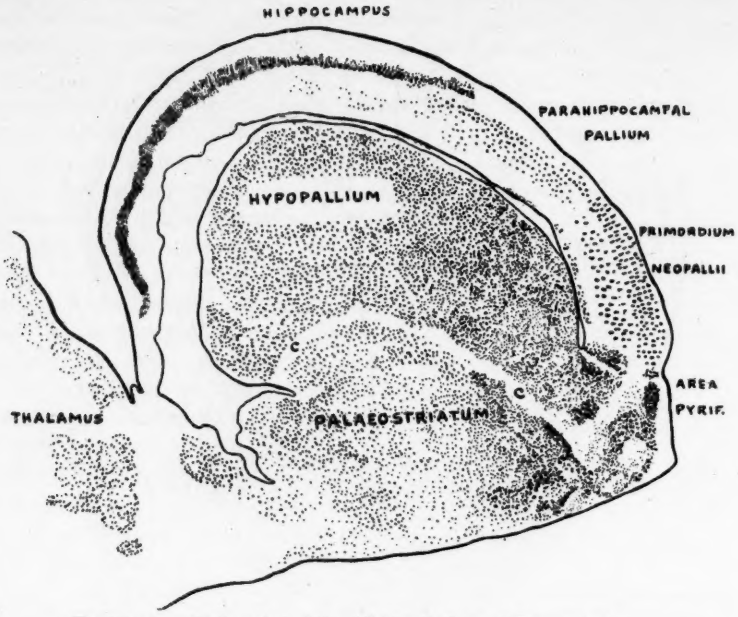


Fig. 12. A sagittal section of the right hemisphere of *Varanus griseus*.

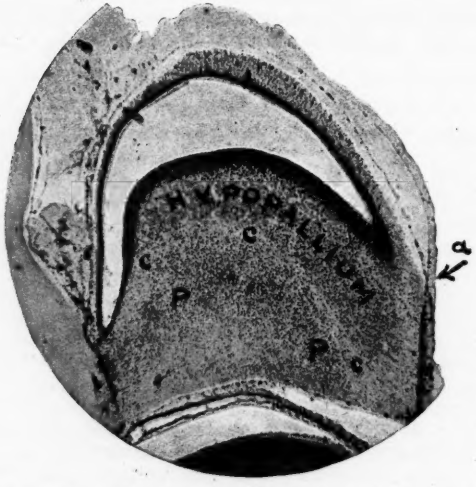


Fig. 13. A similar section through the brain of a foetal *Lacerta viridis*.

to become continuous with the cell masses of the ridge...it does not belong to the corpus striatum" (p. 481). "The dorsal ventricular ridge arises as a thickening of the lateral border of the pallium": "its continued growth causes it to project into the ventricle" (p. 488).

This is precisely the view that I expressed in 1902 and 1910[1]. But both Johnston and I have fallen into error in claiming that the hypopallium does not belong to the corpus striatum, just as Kappers and his collaborators, while they had right on their side when they identified the hypopallium with the major part of the corpus striatum of mammals, fell into the mistake of denying its cortical origin. The chief cause of the wide discrepancy between the two schools of thought has been the failure of both to recognise that a great part of the corpus striatum is composed of modified pallium. Hence we can call the hypopallium "striatal" if we mean that it is the homologue of a great part of the nucleus caudatus and of the putamen of the mammalian brain; but it is not "striatal" in the sense implied by Kappers and de Lange, i.e. it is not wholly, or even mainly, formed as an outgrowth from the palaeostriatum.

If the term "neostriatum" had not been so seriously compromised by de Lange, who applies it in *Varanus* to the anterior part of the hypopallium, and in *Chelone* to a structure which is not hypopallial but really palaeostriatal, it would have been a great convenience to employ it in the sense in which I am using the term hypopallium. In time I hope the confusion created by the Amsterdam school will be cleared away and that Kappers's useful term "neostriatum" can be used without ambiguity for the whole of the hypopallial part of the corpus striatum (inclusive of the hypopallial portion of the nucleus amygdalae).

Towards the end of the eighteenth century John Hunter made a dissection of a turtle's brain, which is now in the Museum of the Royal College of Surgeons in London[2]. In his note upon this dissection he states that there is "an eminence [in what he calls the first or superior ventricle], which extends a little way into the olfactory nerve [i.e. the olfactory peduncle] and runs throughout the whole length of the ventricle." In the diagram (fig. 14), which I have made to illustrate the arrangement of the intraventricular structures in the brain of *Chelone mydas*, the form and relations of Hunter's eminence (*hypopallium*) is displayed.

In 1861 Sir Richard Owen collected such of Hunter's memoranda as had been copied by Clift between the years 1793 and 1800 and published them in two volumes entitled *Essays and Observations*. In a brief reference to the reptilian brain, Hunter states (Vol. I. p. 31) that "the cavities in the cerebrum are larger than in the others, and are similar to those of the higher classes,

[1] *Lancet*, January 15th, 1910, p. 153.

[2] See my reference to Specimen D. 146 on page 124 of the Descriptive and Illustrated Catalogue of the Physiological Series of Comparative Anatomy contained in the Museum of the Royal College of Surgeons of England, vol. II. 2nd edition, 1902.

i.e. they have a large eminence projecting into the cavity, which is the major part of the brain in the Bird."

Writing in the early part of the nineteenth century John Anderson refers to Hunter's eminence in the turtle's brain as "an oblong tubercle analogous to the corpus striatum[1]." When cataloguing the collection of brains in the Museum of the Royal College of Surgeons twenty years ago I made a dissection of the brain of *Chelone mydas*[2], which was placed alongside Hunter's dissection to demonstrate that Hunter's "eminence" is the structure which Edinger had recently labelled "epistriatum." By means of a diagram[3] representing a transverse section through the right cerebral hemisphere of *Sphenodon* I indicated that Hunter's eminence (fig. 14) was derived from the pallium and was the structure which I have called hypopallium in this memoir.

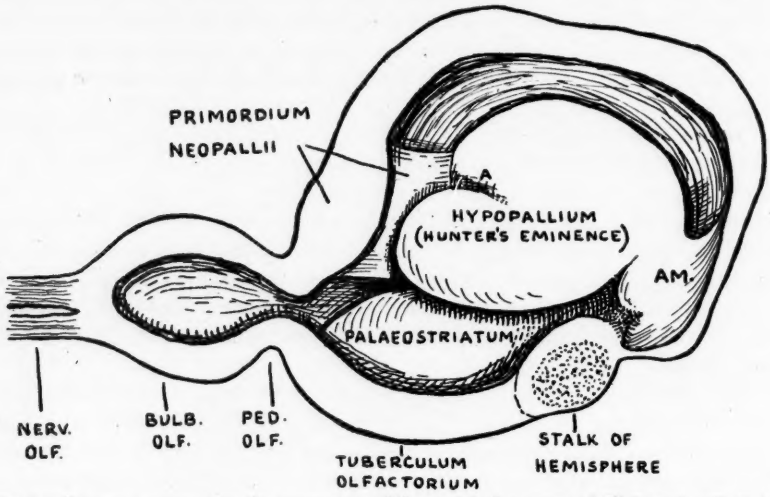


Fig. 14. Diagram representing the appearance of the ventricular aspect of the lateral wall of the right cerebral hemisphere of a turtle (*Chelone mydas*) as displayed by removing the medial wall.

In *Chelone* the hypopallium forms a large oval swelling occupying the greater part of the extensive lateral ventricle. Its anterior end is blunt and notched (*A.*) and is not prolonged forward into a long ridge, as it is in *Sphenodon* (fig. 5). This part of the hypopallium seems to be connected with a thickened band of pallium (primordium neopallii) which extends forward in the lateral wall and forms the anterior end of the dorsal part of the pallium immediately behind the olfactory peduncle. The nature and precise relations of this rudimentary neopallium will be considered later in this note.

[1] Todd's *Cyclopaedia of Anatomy and Physiology*, 1839–1847, vol. III. p. 621.
[2] Catalogue, *op. cit.*, Specimen D. 144, p. 122, fig. 32.
[3] *Op. cit.*, fig. 33, p. 123.

Posteriorly the hypopallial eminence is continuous with a less prominent and irregular mass (*A.M.*) which is attached by a broad base to the postero-lateral wall of the hemisphere in the region of the postero-ventral recess of the ventricle, the first rudiment of the inferior cornu. The constitution of this little mass (*A.M.*) is similar to that of the rest of the hypopallium, of which it is merely the caudal extremity. It represents the hypopallial element of the nucleus amygdalae of mammals and is pallial in origin.

The peculiar relations of the primordium neopallii in the Chelonia have been the cause of much misunderstanding and confusion, especially in the

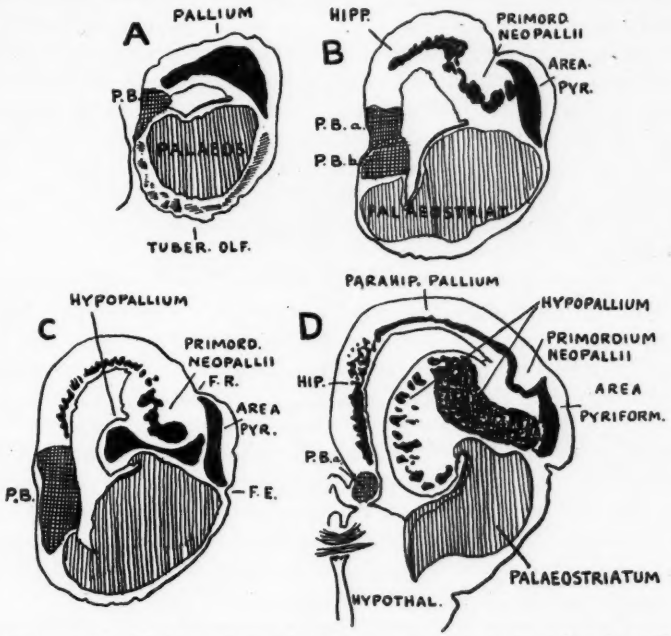


Fig. 15. Diagrams (modified from J. B. Johnston's memoir on the brain of *Cistudo*) to illustrate the arrangement of the grey matter in four sections of the anterior part of the right cerebral hemisphere of a turtle.

writings of Edinger and his collaborators. It is by no means easy to unravel the complex pattern of the anterior pallial area in such Chelonia as *Chelone* and *Testudo*. But the admirable account given by Johnston of the cell masses in the brain of an American turtle, *Cistudo carolina*[1], makes the arrangement quite clear.

In fig. 15 I have attempted to express in diagrammatic form four stages in the differentiation of the pallium as revealed (in Johnston's series of beautiful drawings) in sections of the anterior end of the hemisphere of *Cistudo*.

[1] *Op. cit.*, J. C. N., vol. xxv. 1915, p. 393.

The anterior end (*A.*) shows a simple arrangement, which closely reproduces the most primitive features of the Vertebrate hemisphere as this is displayed in the Elasmobranch and Cyclostome fishes. A large part of the section is composed of the old basal ganglion or palaeostriatum, the superficial layer of which has been differentiated in a cortex-like manner to form the tuberculum olfactorium. The dorsal cap of pallium is an unbroken column of cells, which on being traced backward (*B.*), becomes differentiated into three parts, an inner (*HIPP.*), an intermediate (*PRIMORD. NEOPALLII*) and a lateral (*AREA PYR.*). Further back (*C.* and *D.*) two other pallial areas become differentiated, the parahippocampal pallium and the hypopallium.

The points to which I wish to direct special attention are (1) the fact that the primordium neopallii is derived from the pallial area on the dorsal side of the area pyriformis; (2) that it forms a swelling in the wall of the ventricle (*B.*) which joins that formed by the hypopallium (*C.*), and like the latter consists of a bending-in of the pallium (*B.*); and (3) that the hypopallial cortex is formed from the lateral edge of the pallium (*D.*) on the ventral side of the pyriform area, whereas the latter itself forms the lateral border further forward (*B.*).

The inbending of the cortical bands in the primordium neopallii and the hypopallium respectively bring these structures into close proximity (*C.*) on the deep aspect of the pyriform area, which remains upon the surface when its dorsal margin becomes separated from the primordial neopallium and its ventral margin from the hypopallium.

Before discussing the meaning of these peculiar arrangements of the pallium in the Chelonia, I want to mention a feature of the brain in Crocodilia and Aves which has long been an enigma. In these closely related animals the primordium neopallii forms a very large swelling in the anterior part of the lateral ventricle which becomes so completely fused with the hypopallium that it seems to form part of it. The true state of affairs is clearly shown in an excellent memoir by Elizabeth Caroline Crosby[1].

Thus the homologue of the neopallium of mammals is found in the anterior part of the so-called "corpus striatum" of crocodiles and birds. The arrangement of the pallial areas in the turtle (fig. 15) affords the clue for the interpretation of this enigma.

It is now possible to appreciate the amazing confusion in the use of the term "epistriatum." In the memoir in which Edinger[2] first introduced this term in 1896 it was applied in the brains of *Varanus* and *Python* (Taf. II, figs. 2 and 4) to the *posterior* part of the structure which is called hypopallium in these notes. But in the same plate the term is applied in the brain of *Chelone* to the primordium neopallii (fig. 6), to the dorsal part of the *anterior*

[1] "The Forebrain of Alligator Mississippiensis," *Journal of Comparative Neurology*, vol. XXVII. 1917, especially figures 5 and 6.

[2] L. Edinger, *op. cit., supra.*

extremity of the hypopallium (fig. 5), and to the upper part of the whole length of the hypopallium, excluding the lower part, which is called "mesostriatum" (fig. 7). Not content with this use of the term in the three or four different and conflicting senses, in the following years Edinger gave it a fifth meaning by applying it to a structure in the bird's brain which is not identical with any of the three parts of the reptile's brain which he had already called "epistriatum." Then he used it for a part of the Amphibian brain which is not pallial at all, and for a structure in teleostean fishes which is the homologue of the whole pallium. To these seven meanings yet an eighth was added by restricting the term in mammals to the nucleus amygdalae. Other writers have attempted to apply Edinger's term and, selecting at random from a list which in one or other of the senses includes most parts of the hemisphere,

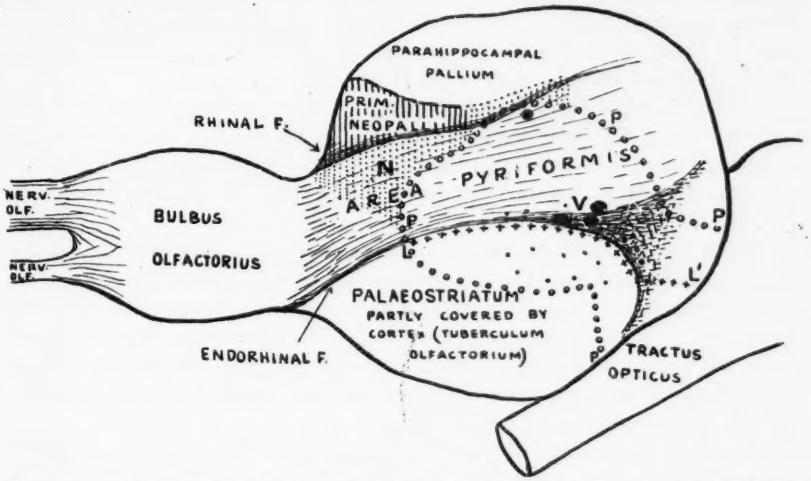


Fig. 16. Diagram of the lateral aspect of the left cerebral hemisphere of *Chelone mydas*. + + + + + line of bending in of the pallium to form the hypopallium, the extent of which is indicated by the line of circles ooooooo. *N*. the place where the primordium neopallii is overlapped by the area pyriformis. *V*. the three large foramina for the lateral striate vessels.

have added materially to the chaos by applying this much abused label to other structures not included in Edinger's formidable list. The time has surely come to discard once for all a term which is fruitful of so much confusion. Edinger has been equally reckless in his abuse of the term "area parolfactoria," which he has used for a great variety of different structures; I refer to it here because in the brains of the Chameleon and the bird he uses it for part of the palaeostriatum.

In the foregoing remarks I have referred to the fact that in the Chelonian brain two distinct infoldings of the cortex occur, to form the hypopallium and the primordium neopallii respectively. The relative positions of the intraventricular protrusions thus caused is shown in fig. 14, and in the four

diagrams in fig. 15 the arrangement of the pallium of which these thickenings are formed is explained in transverse sections. To aid in the understanding of this puzzling arrangement I have constructed a diagram (fig. 16) to display the positions of these structures in relation to the lateral aspect of the hemisphere.

Passing obliquely across the lateral aspect of the hemisphere a slightly raised band, the area pyriformis, is seen proceeding backwards from the olfactory peduncle. It is the imperfectly differentiated homologue of the pyriform lobe of the mammalian brain, and like it is separated below from the palaeostriatal area (partly covered by the cortex of the tuberculum olfactorium) by a shallow furrow or endorhinal fissure. Along its upper border there is a faintly marked depression which is the earliest form of the rhinal fissure. The line along which the cortical band bends inward to form the hypopallium (the position of which is roughly indicated by small circles) corresponds to the endorhinal fissure (compare fig. 15, *C.* and *D.*, the furrow marked *F.E.*), beginning in front (at the place marked *L*) and passing backward (along the line of crosses in fig. 16 as far as *L'*).

The infolding of the primordium neopallii, however, takes place *above* the anterior end of the area pyriformis (fig. 15, *B.*, *C.* and *D.*), corresponding to the line of the rhinal fissure (fig. 15, *C.*, the depression marked *F.R.*). But the primordium neopallii passes downward under cover of the area pyriformis (fig. 16, *N.*; compare fig. 15, *C.*) to meet the hypopallium.

When the primordium neopallii undergoes further development and becomes transformed into the true neopallium of mammals it becomes enormously expanded. The infolding found in certain of the Sauropsida (Chelonia, Crocodilia and Aves) does not occur, but the expansion is expressed in a great increase in its superficial area. It pushes the parahippocampal pallium on to the inner face of the hemisphere so that eventually it becomes relegated to the gyrus cinguli in the human brain.

Ariëns Kappers expressed the opinion[1] that "the striatum proprium undergoes a significant expansion in reptiles, in virtue of the fact that it becomes indirectly connected with the trigeminal fillet by means of a new double connection with the nucleus rotundus thalami—the tractus fronto-thalamicus —which caused the development of a mass of tissue at the frontal pole (neostriatum or pars medio-dorsalis striati proprii)." My objection to this statement is twofold. The neostriatum (to adopt Kappers's later practice of omitting the hyphen from this term) is not derived from the striatum proprium, which Kappers elsewhere calls the palaeostriatum, but from the pallium. Secondly, the presence of fibres ascending from the thalamus to the cortical area which becomes transformed into the neostriatum is not a new development in reptiles. Such fibres can be detected proceeding to the homologous area (i.e. the lateral edge of the pallium) in Amphibia, as the

[1] "Die Phylogenese des Rhinencephalons, des Corpus striatum und der Vordehirn-Commissuren," *Folia Neuro-biologica*, Bd. I. 1908, p. 268; compare also his note in *Anatomischer Anzeiger*, Bd. XXXIII. 1908.

researches of Pedro Ramon and Rubaschkin (quoted by Kappers himself, *op. cit.*, p. 206) have demonstrated. These observations have been confirmed by Judson Herrick, who fully appreciated their significance when he wrote[1]: "The nucleus sphaericus (of Adolf Meyer and Edinger, occipito-basal lobe of C. L. Herrick, epistriatum of Edinger and Kappers) in reptiles may now be compared, in a general way, at least, on the basis of its fibre-connections, with the pars dorso-lateralis [the lateral part of the pallium] of the frog-brain and the pyriform lobe and amygdala of lower mammals."

In other words the hypopallium of reptiles is homologous with a pallial area in Amphibia, and not with a palaeostriatal structure, as Kappers and his school maintain.

Hence the distinctive innovation in the reptilian brain is not the first appearance of this thalamic tract passing to the pallium, because such fibres are already present not only in Amphibia, but also in Dipnoi and Fishes, as Kappers and Johnston, among others, have demonstrated; but it is the great increase in number of the fibres of the tract in reptiles that determines the sudden expansion of the pallium and the development of the hypopallial eminence.

The significance of these facts should now be apparent. The most primitive vertebrates are already provided with a definite if very rudimentary pallial formation, a basal ganglion which is the representative of a part of the corpus striatum of more highly developed forms, and a cortical cap covering the ventral surface of this palaeostriatum, which is a well-developed tuberculum olfactorium. Into all parts of the surface of the earliest cerebral hemisphere olfactory tracts of the second or third order make their way; and efferent fibres arise both from the palaeostriatum and from the primordial pallium to establish connexions with the hypothalamus and epithalamus; and through the intermediation of these structures the influence of olfactory impressions can be brought to bear upon the motor mechanisms of the mid- and hind-brain, and through them upon the spinal cord, and so enable the animal's behaviour to be influenced by smell.

Although the primitive cerebral hemisphere is essentially a receptive centre for smell impressions and a mechanism for transferring the effects of olfactory stimulation into the appropriate channels for directing the animal's movements, it is of fundamental importance to remember that even in the lowliest vertebrates tracts of other kinds make their way into all parts of the hemisphere, primordium pallii, palaeostriatum and tuberculum olfactorium, and provide the means whereby tactile, gustatory and visual, and other kinds of stimuli may modify the nature of the response excited in the cerebral hemisphere by the application of adequate chemical stimuli to the olfactory cells.

A noteworthy increase in the number of the tactile and optic fibres pro-

[1] "The Morphology of the Forebrain in Amphibia and Reptilia," *Journal of Comparative Neurology*, vol. xx. 1910.

ceeding from the thalamus to the lateral border of the pallial formation, and probably the addition of a new thalamo-cortical tract conveying acoustic impulses, was responsible for the origin of the reptiles from a primitive Amphibian (Stegocephalian) stock. The immediate effect of the admission of this fuller representation of touch, vision and hearing into the domain of cerebral functions was manifested in an expansion of the cerebral cortex, and in the animal's behaviour by a more varied power of adaptation to circumstances, which was due to a fuller blending of the influences of smell, taste, touch and vision and especially a noteworthy increase in the ability to learn by experience.

The great thalamo-cortical tracts first made their way into the lateral part of the pallial formation. At first the function of this part of the pallium, like all the rest, was primarily olfactory; but as the non-olfactory thalamic radiations increased in dimensions and the cortex expanded to act as a receptive and co-ordinating mechanism for them, the time arrived when the balance of influence in certain areas was transferred from the olfactory to the non-olfactory elements. In accordance with Ariëns Kappers's principle of neurobiotaxis the part of the pallium that came under the influence of these thalamic radiations underwent a relative change of position; the cortical area affected seemed to be attracted towards the fibres coming from the thalamus, from which they received their stimuli. A great intraventricular ridge was thus formed from the lateral part of the pallium which during the ontogenetic growth and expansion of the hemisphere appeared to be tied to the thalamus by the physiological bond of the influence of the thalamo-cortical fibres.

But, the thalamic fibres pass beyond the cortical area that is bent inward to form the hypopallium, especially at the anterior end of the hemisphere where a localised area of pallium (fig. 16) is stimulated to undergo a new and significant transformation, which eventually results in the formation of the neopallium. In the midst of the area affected by these new influences there is a band of pallium which maintains its superficial position and is not drawn toward the ascending thalamic fibres, as the hypopallium and the primordium neopallii are. This is the area pyriformis which, in virtue of Kappers's principle of neurobiotaxis, remains upon the surface because the lateral olfactory tract lies upon it and constitutes the main source of its afferent impulses. Hence the pyriform area remains upon the surface (fig. 16) as near as possible to the tract of fibres which pour olfactory impulses into it, while the hypopallium and the primordium neopallii seem to move towards the main source of their stimuli, i.e. the thalamic tracts.

One fact in connexion with this discussion I did not appreciate until a few months ago. The hypopallium of reptiles persists in the mammalian brain where it forms the greater part of the caudate nucleus and of the putamen of the lenticular nucleus, the globus pallidus representing the major portion of the palaeostriatum. In the development of the mammalian brain the phylogenetic history of the corpus striatum is clearly revealed.

A long series of investigations of the embryology of the mammalian brain[1] in almost every Order, from the Monotremata to the Primates, has demonstrated that at a certain stage of development (roughly corresponding to the period[2] covered by the end of the third to the sixth month of foetal life in the human embryo) there is a clearly defined separation of the corpus striatum into a palaeostriatum and a hypopallium (which might be called "neostriatum," if Kappers had not used this term in a somewhat different sense), and traces can be found of the inbending of the cortical band of cells at the ventral margin of the pyriform lobe, just as in the reptilian brain.

In fig. 17 I have constructed a diagram to illustrate the arrangement of these structures in a human embryo at the fourth month. The cortical band in the pallium bends inward at the situation of the lateral striate artery (*A.*), just as it does in the brain of *Sphenodon* (fig. 1). The upturned cortical band becomes the claustrum (*CL.*); and it passes into the rest of the hypopallium (*H.*), from which most of the caudate nucleus and the putamen are formed. The globus pallidus and a small part of the caudate nucleus are derived from the palaeostriatum which is a distinct ridge at this stage in the development of the human embryo.

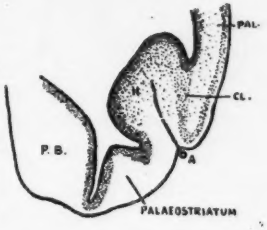


Fig. 17. Diagram representing the arrangement of parts in the lower part of a transverse section of the right hemisphere of a human foetal brain at the fourth month. *A.* lateral striate artery. *H.* hypopallium. *CL.* claustrum. *P. B.* paraterminal body. *PAL.* pallium.

This arrangement can also be demonstrated in the adult brains of such small mammals as *Notoryctes*, *Perameles*, *Dasyurus*, *Chlamydophorus*, and many others which I have examined.

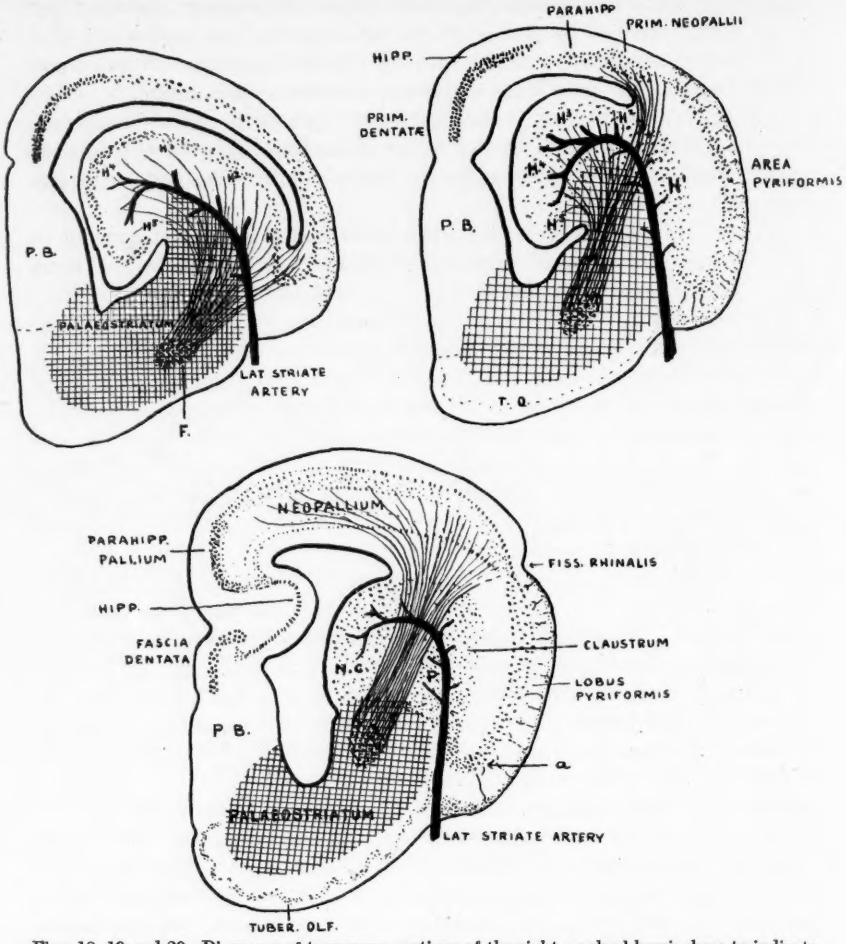
The history of this transformation can be expressed in diagrammatic form (figs. 18, 19 and 20).

One of the most remarkable items of evidence in corroboration of the reality of the homologies expressed in these diagrams is the constancy of the position and relations of the lateral striate artery. At the place where the middle cerebral artery crosses the endorhinal fissure (see fig. 16, *V.*) there is given off in the turtle's brain an exceptionally large perforating artery (or several arteries) which pass into the brain along the boundary line between the palaeostriatum and the hypopallium (compare figs. 1, 17, 18, 19 and 20). In mammals of every Order one or more large arteries enter the brain at the identical spot, i.e. the postero-lateral corner of the tuberculum olfactorium, immediately to the inner side of the olfactory tract and in front of the tubercle of the olfactory tract. In any mammalian or reptilian brain this arrangement will

[1] See Ziehen in Hertwig's *Entwickelungslehre der Wirbeltiere*, II. 3.

[2] G. Retzius, *Das Menschenhirn*, Taf. VI.; compare also Percival Bailey, "Morphology of the Roof Plate of the Forebrain and the Lateral Choroid Plexuses in the Human Embryo," *Journal of Comparative Neurology*, vol. XXVI. 1916, fig. 24.

be found. It is shown by Retzius in the human brain[1], and I have found it in members of almost every mammalian Order. In fig. 21 (depicting part



Figs. 18, 19 and 20. Diagrams of transverse sections of the right cerebral hemisphere to indicate how the primitive reptilian arrangement (fig. 18) becomes transformed in the evolution of the primitive mammal (fig. 20), and especially the way in which the hypopallium of the reptile (H^1, H^2, H^3, H^4 and H^5) becomes converted into the upper part of the nucleus caudatus (N.C.) (the lower part of which is palaeostriatal), putamen (*P.*) of the nucleus lenticularis and claustrum.

of an elephant's brain) the three large foramina (*V.*) are shown at the place mentioned. The artery that enters at this point in the human brain is the vessel which Charcot called "the artery of cerebral haemorrhage."

[1] *Das Menschenhirn*, Taf. XXXII.

If the relations of this vessel be compared in a series of reptilian and mammalian brains they afford striking corroboration to the hypothesis that a large part of the mammalian corpus striatum is homologous with the reptilian hypopallium and is therefore cortical in origin.

In 1896 Koelliker[1] referred to the nucleus caudatus and putamen of the nucleus lenticularis as parts of the cerebral cortex ("Theile der Hirnrinde") and he refers to the earlier work of Ganser on the brain of the mole in which the statement is made that the corpus striatum is disposed like a cortical structure.

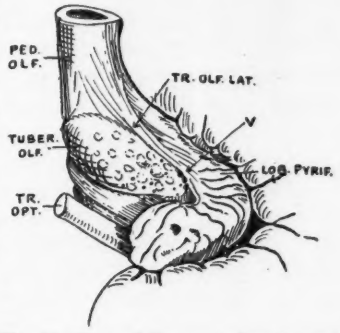


Fig. 21. Part of the ventral surface of the left hemisphere of an elephant to show the position (*V.*) of the three large vascular foramina (compare fig. 16).

There is one further point that I must mention. In all these reptilian brains it is the palaeostriatum which is attached to the thalamus and hypothalamus. A narrow band of palaeostriatum proceeds backward in the floor of the hemisphere above the stalk (strio-thalamic junction) and separates the thalamus from the hypopallium (neostriatum). The same arrangement can be detected in the mammalian foetus. Hence it is certain that the palaeostriatum must form a part, though probably a very insignificant part, of the tail of the caudate nucleus.

In a later communication I shall give an account of the fibre-tracts of the corpus striatum and discuss the wider significance of the facts set forth in these notes.

In conclusion I must express my acknowledgement to the late Mr Martin Woodward, who in 1897 gave me the brain of *Sphenodon*, the study of which first directed my attention to the problems discussed in this note. For other specimens of this extremely important type of brain I am indebted to the late Professor G. B. Howes, F.R.S., to Dr Hans Gadow, F.R.S., to Professor Arthur Dendy, F.R.S., to Mr Herbert Bolton, M.Sc., Director of the Bristol Museum and Art Gallery, and to Dr W. M. Tattersall, Keeper of the Manchester Museum. For the opportunity of examining series of sections of embryos of *Talpa*, *Canis* and *Homo* I am indebted to Professor E. Fawcett.

[1] *Handbuch der Gewebelehre des Menschen*, II. Bd. 1896, p. 613.

THE FORMATION OF THE DUODENAL CURVE

By J. ERNEST FRAZER, F.R.C.S.,

St Mary's Hospital, Professor of Anatomy in the University of London

In a paper dealing with intestinal rotation, and written a few years ago, Dr R. H. Robbins and I showed that the duodenum is not involved in this rotation, and we therefore treated the production of its curve very shortly. We pointed out that this portion of the intestine is at first very short, and that it is subsequently elongated in accordance with, and curved out by, the growth of the

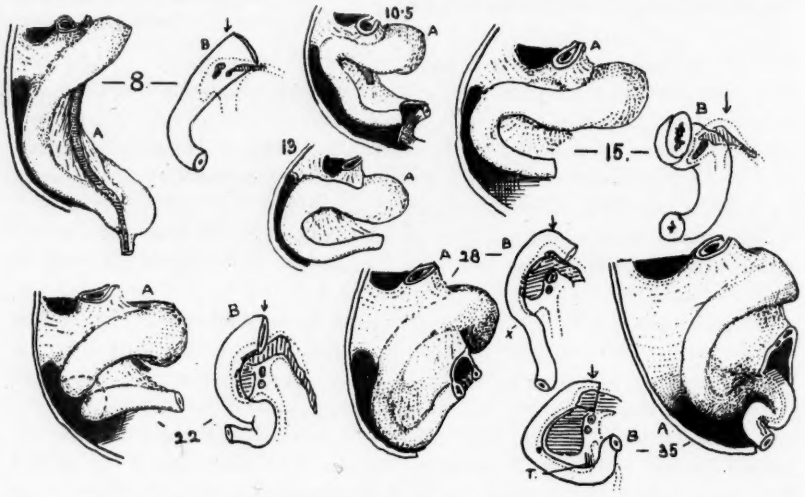


Fig. 1. The duodenum throughout the "first stage" of intestinal development. *A*, side view, *B*, front view. The numerals give the size of embryo in millimetres. See text.

head of the pancreas. From an early stage it is attached to the dorsal wall by the mesoduodenum, in which the head of the gland grows, and the bowing out of the tube takes place round this base of fixation; we stated, however, that we were not certain whether there might not be some later secondary fixation of the extreme terminal part of the gut known as the duodenum. I propose now to give some further details bearing on the matter.

In the figures I have illustrated the parts seen at several stages. The younger specimens were mostly drawn from models, the later ones directly.

In the former the duodenum is shown from the left (*A.*), but in some cases additional projections from the front are added (*B.*). Measurements (sitting-height) are given in numbers of millimetres.

At 8 mm. (fig. 1) the duodenum can be recognised as that part held by the mesoduodenum, and is a short and nearly straight tube directed caudally and dorsally, and likewise towards the right, as can be seen in the frontal projection. It is continuous below with the intra-abdominal portion (duodeno-umbilical loop) of the short U-loop of the gut.

The mesoduodenum may be defined for our present purposes as a thickened region of the common median dorsal mesentery, supporting that part of the tube immediately distal to the stomach. It occurs just below the pouch of the bursa omentalis, of the opening of which it forms the lower boundary or floor. Hence the lower part of the opening is seen in the drawing just above the mesoduodenum, and the vitelline vein, passing through the mesoduodenum behind and to the left of the gut, runs up to the liver (portal vein) in front of the bursal opening; that is, the upper "edge" of the mesoduodenum becomes continuous, dorsal to the line of the tube, with what is the free edge of the gastro-hepatic omentum. Caudally, the mesoduodenum stands out well, and a small recess (inter-mesenteric recess) exists between its rounded caudal border and the median mesentery; this recess persists to a late period.

In the frontal projection the position and attachment of the mesoduodenum is shown by a dotted line, and its continuity with the bursal floor is seen on the one hand, and with the general mesentery on the other, with the inter-mesenteric recess intervening. The duct openings are indicated by dots, with the small pancreatic growths associated with them; the body of the gland is seen to be already invading the bursal wall, but the head, very small, is in the mesoduodenum itself. The vitelline vein is not shown, but runs behind and to the left of the upper duct opening.

In the 10·5, 13 and 15 mm. specimens there does not seem to be much growth of the duodenum apart from the general increase in size of the parts, but there is a more pronounced dorsal direction. This seems to be due to growth of the stomach, and possibly of the liver; the frontal projection of the 15 mm. state appears to show this, for the gastric end is more to the right, and the duodenal direction seems to be horizontally to the dorsum and inwards. The mesoduodenum is apparently a little broader, but the head of the pancreas has not grown at the same rate as its body, for this last stands up well towards the floor of the bursal opening and is just apparent above and behind the duodenum.

The 22 mm. stage shows a definite duodenal curve, convex to the right, seen in the front view; an 18 mm. model, not drawn, shows a much less marked tendency toward the same curve. This curve is evidently associated with the decided increase in size of the head of the pancreas, which now occupies the greater part of the right portion of the mesoduodenum, extending

down in it but not reaching its lower end. The duodenum now stands out to the right to some extent from its attachment, rolled out, so to speak, by the growth on its inner side, so that the duct openings are more definitely postero-internal than in previous stages. The tube has increased correspondingly in length; the first increase would seem to be mainly in its proximal part, but, as the head grows, the portion distal to the ducts extends more rapidly. Its distal end is turned in toward the mesentery and joins the duodeno-umbilical loop through a twisted U-shaped kink, which I have already shortly discussed in the previous paper and need not notice further.

The head is larger in the 28 mm. specimen, and the curve more pronounced in correspondence, but its effect is spoilt by the absence of the U-shaped kink distally; in the direction of the tube there is a decided indication (*x.*) of the end of the duodenal region, and it is quite possible that there may have been a bend below this in the fresh state, but in the model the tube passes directly, at the site of the angled junction, into the duodeno-umbilical loop. The head of the pancreas is now for the first time apparent ventrally, and this is necessarily associated not only with the opening out of the duodenal curve but with lessening of the general dorsal direction of the tube.

A marked advance is seen at 35 mm. Here the duodenal curve would at first sight appear almost complete, and is associated with a large pancreatic head; as we shall see shortly, such reading of the appearance would not be correct, but at any rate it is not unlikely that the specimen exhibits, as an individual variation, a state rather more advanced than others at this stage. The 40 mm. specimen in fig. 2 shows a more angled curve, with a less wide head, but the depth of the head is well-marked. Treitz' band (*T.*) is indicated in the frontal figure of 35 mm. I have not been able to recognise it definitely at an earlier stage. Its situation here shows the fallacy of appearances in this specimen, for it is evident that the hinder limb of the "kink," as seen in the frontal drawing, is not the ascending piece of the duodenum; this will have to be formed later and more proximally, and is indicated in the 40 mm. specimen.

In this, as in the others, the intermesenteric recess is evident, and its presence shows conclusively that the duodenum remains attached to, and only held by, the mesoduodenum; as it curves out, it stands out from the mesoduodenum, which is only continuous with it near its inner edge, except at its upper end. The curve is evidently due to the growth of the mesoduodenum and pancreas; the former enlarges ahead of the latter in its lower part, as may be seen in the figures, and the part as yet unoccupied by the pancreas contains a vascular plexus which is the forerunner of the lower pancreatico-duodenal loops, and quite distinct from the vascular supply to the next succeeding part of the gut.

We can see then that the duodenal curve is well advanced in formation before the bowel enters the abdomen and undergoes its "rotation" therein. This occurs about 40 mm.; in the 40 mm. specimen figured the gut was in the

belly, a position which it had probably just taken, perhaps even during preparation, but manifestly the state of the duodenal curve has nothing to do with this. The model shows, however, that the duodenum as a whole had moved somewhat to the left, swinging on the dorsal attachment of the mesoduodenum.

This is easily understood and to be expected. The previous figures and those in the original paper show that the "kink" in the duodeno-jejunal region is pressed against the median mesentery (mesocolon). When this structure moves dorsally and to the left as a result of the entry of intestinal coils from the umbilicus, it not only permits the region of the "kink" to follow

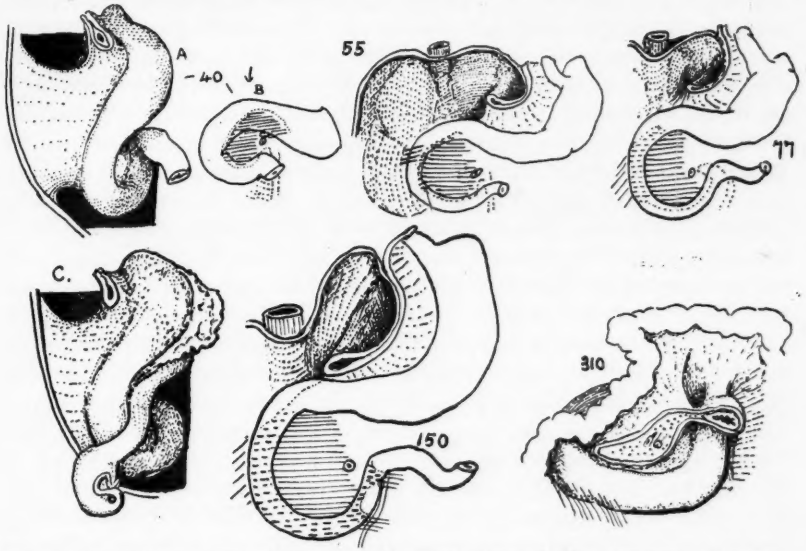


Fig. 2. Side and front views of 40 mm. model. Front views of older specimens. *C*, a semi-diagrammatic drawing to show position of colon at end of second stage. In the later stages shown, pancreas is indicated by horizontal shading, adhesions by oblique shading and interrupted lines.

in the same direction, but, through its continuity with the mesoduodenum, tends to swing this somewhat also to the left; hence the changed relation, especially of the distal part, to the middle line as indicated by the arrows in the frontal views.

As in many other parts of the body, individual variations become more apparent as the specimens become older, and the later history of the duodenum, including its final fixation, is not so smoothly written in the foetus as the earlier stages seem to be in the embryo. I have put in fig. 2, however, a few drawings from the dissections I have made which will give, I hope, a fairly accurate if rather general idea of these later happenings.

The progressive enlargement of the duodenal curve goes on as before,

with variations. The few stages shown illustrate this and the association between it and the pancreas and mesoduodenum. But the secondary attachments of this portion of the gut are still more variable in their occurrence; presumably they wait for their time till the curve is complete, and then find the governing factors variable—but what these factors may be, other than the teleological call for support mechanically, I have not been able to ascertain.

The commencement of the ultimate fixation occurs when the (originally umbilical) colon comes back across the "neck" of the intestinal mesentery and thus lies in front of the duodenum. It seems to be fairly constant (fig. 2, *c.*) in its position here, so far as my observations go, and is found running downwards and outwards, parallel to and just below the upper part of the duodenum, and then crossing it to come into relation with (caecum) the kidney. If this drawing is compared with that of the 40 mm. specimen above it, it is clear that the site of crossing is opposite the lower part of the mesoduodenum as seen from the right. Here occurs the first secondary fusion affecting the duodenum, soldering it and colon and kidney together at this level. In all my specimens the colon has not come into position at a *lower* level, so that, depending on these, it seems justifiable to regard the original right free surface of the mesoduodenum as being visible in the adult above the level of the crossing colon. This surface extends up to the margin of the opening into the omental bursa, as seen in the drawing. The bursal opening is not the foramen of Winslow, but is marked, so far as its floor is concerned, by the lower pancreatico-gastric fold[1]; in the embryonic state the hepatic artery lies in the lower edge of the opening and has the base of the intra-bursal liver process resting on it (papillary process of Spigelian lobe). The upper part of this surface of the mesoduodenum, then, is continued through the floor of the foramen of Winslow to the line of the hepatic artery. The foramen of Winslow is a late formation, probably due to the increase in size of the inferior cava, and possibly also of the liver and pancreas; this can be understood from the figures, and no further stress need be laid on it or on the simultaneous addition of a "vestibule" to the small sac, not derived from the omental bursa.

The lower aspect of the mesoduodenum, however, remains unattached behind the transverse part of the duodenum, which is fastened to its front and lower margin. This may be understood from the 55 mm. drawing, where the mesoduodenum evidently comes down to a level lower than that of the crossing colon, and an open groove or sulcus underlies the duodenum distal to this line. This is the same as saying that, beyond the level of the colon, the duodenum is free from attachment on its posterior surface.

Increasing areas of attachment are indicated in the 77 and 150 mm. specimens, and, speaking generally, the adhesions seem to be developed first near the colon and to extend distally. One cannot recognise the intermesen-

[1] I mention this fold in deference to the view that it marks the mouth of the bursa omenti majoris. My own view is that the band is produced later, and that the line of the hepatic artery is the only original and proper line to take.

teric recess with certainty as soon as the adhesions affect the ascending portion of the tube, but before this occurs it is quite distinct (60–70 mm.) and shows definitely that the duodenal curve is completed round the mesoduodenum and head of the pancreas. In the 77 mm. drawing there is a recess of doubtful value; probably the true recess has been obliterated by the adhesions which have taken place behind the gut.

No useful purpose would be served by describing or figuring the various adhesions met with in the foetuses examined. The general conclusion arrived at was, as already intimated, that these were last formed and most variable in the region of the ascending part; two are shown in the 150 mm. specimen, overlying the inferior mesenteric vein, of which the immediate causation is not very evident, although the mechanical call for their existence may be plain enough. The connection with the common folds and fossae in the neighbourhood is obvious. In the 310 mm. specimen there is a marked and extensive adhesion below the first half of the transverse part, which would become continuous[1] with the mesentery when this is attached to the front of the duodenum; a sulcus, unmodified by any adhesions, lies behind the rest of the duodenum.

This drawing is introduced, however, to show a secondary attachment of the highest part of the tube to the transverse mesocolon; the true continuity between mesoduodenum, mesentery, and mesocolon lies to the right, where it is clearly seen. A small fossa (? Gruber's fossa) separates the two folds. Evidently, in some cases at least, the adult duodenum may include, at its extreme end, a very short piece of gut which is not attached in the embryo by the mesoduodenum, and becomes fixed in position by means of secondarily acquired adhesions.

Enough has been said to show the possibility of explaining the occurrence and site of the different fossae—with the exception of the paraduodenal, about the origin of which I have nothing to advance—as mere variations in the adhesions formed in relation with the duodenum distal to the crossing of the colon. While the duodenum as a whole is curved out by the enlarging head of the pancreas and is primarily held only by the mesoduodenum, the lower part of it, below the crossing of the colon, is the part which projects most beyond the position of the base of attachment and is secondarily fixed by late adhesions. Immediately distal to the crossing of the colon these adhesions will, still later, be reinforced by the fixation of the mesentery across the face of the duodenum; this, as pointed out in the earlier paper, is really a secondary adhesion of the "mesocolon of the loop"—as is also in all probability the first adhesion at the level of the crossing. Thus, from the colon to the "line of attachment of the mesentery" across the duodenum, the gut is more firmly fastened down, and it is beyond this line that the variations in the secondary bands become apparent.

[1] This fold in the 310 mm. foetus is probably adherent mesocolon and hence differs from the attachments shown in 150 mm. It would lie superficial to them and would not vary with them

V

NOTE ON THE REPTILIAN HEART

By EDWIN S. GOODRICH, F.R.S.,

Fellow of Merton College, Oxford

In a recent paper on the Classification of the Reptilia (1) I drew attention to the significance of the structure of the heart, and concluded that the Amniota diverged into two branches: the Sauropsidan branch culminating in the Aves, and the Theropsidan branch in the Mammalia. It was pointed out that although the highest forms in each of these branches are provided with a four-chambered heart, yet these hearts differ in fundamental structure, and must have been independently developed along diverging lines from a more primitive three-chambered heart with symmetrical aortic arches. The final conclusion was therefore reached that all living reptiles belong to the sauropsidan branch and must have been derived from a common sauropsidan ancestor in which the heart was already built on the sauropsidan plan, with the aortic trunk subdivided (the left aortic arch crossing the right), and most of the arterial blood passing through the right arch to reach the dorsal aorta. Thus, when an interventricular septum is completed, the arterial blood passes from the left ventricle into the undivided aortic trunk in the mammal, and into the right aorta in the bird. When, as in the crocodile, the left aortic arch persists it receives venous blood only from the right ventricle.

In the paper referred to above, the heart of the various orders of living reptiles was not described in detail; but diagrams were given, one of which purports to show the relation of the arches to the chambers in the Rhynchocephalia, Lacertilia, Ophidia, and Chelonia. O'Donoghue, in a contribution which appeared last year in this journal (5), while accepting my general conclusion that no modern reptilian heart can lead to the mammalian structure (5, p. 479), takes exception to my statement that "in the Reptilia the interventricular septum tends to divide the chamber into a left cavity leading to the base of the right systemic arch, and a right cavity leading to the base not only of the pulmonary, but also of the left systemic arch" (1, p. 271). He admits that this statement is correct with regard to the Crocodilia and Chelonia; but maintains that it is "incomplete and indeed somewhat misleading" as regards Lacertilia and Ophidia. But O'Donoghue's own statements, when discussing the heart of these two orders, are so extraordinary that they must be quoted in full. On p. 478 he writes:

"Thus the conditions in Ophidia and Lacertilia are quite different from what is implied by Goodrich both in the extract given above and in the dia-

gram. The ventricle in these two groups, containing by far the greater number of living species of reptiles, is indeed partially divided into a right and left chamber, but the two systemic arches came off from the right side and the pulmonary arch alone comes off from the left. There is thus a considerable difference in the relation of the septum to the arterial trunks between the Ophidia and Lacertilia on the one hand and the Crocodilia and Chelonia on

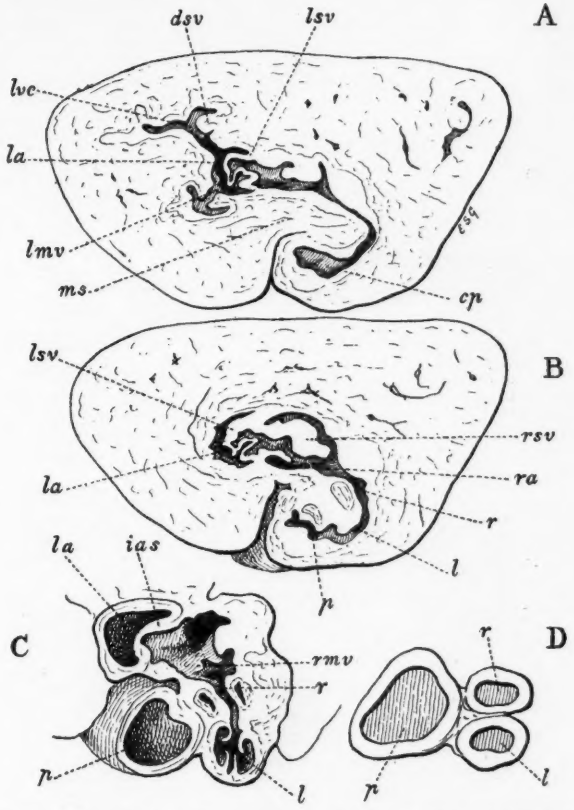


Fig. 1, *A*, *B*, *C*, *D*. Chelone midas. Transverse sections through the ventricle and base of the aortic arches seen from behind (posterior view) with dorsal edge above and ventral edge below. *A* is the most posterior, and *D* the most anterior section.

the other. Not only is there a greater twist on the arterial trunks, which leave the top of the heart in relatively the same position, while the pulmonary leaves the ventricle more to the right in the latter, but the septum is actually situated on opposite sides of the pulmonary artery. In Ophidia and Lacertilia it lies between the pulmonary and left systemic, while in Crocodilia and Chelonia it lies between the pulmonary and right systemico-carotid."

"Another striking and important difference which has not been emphasised formerly is that, whereas in the Crocodilia and Chelonia, as in birds and mammals, the aerated blood is poured into the left side of the ventricle, in Ophidia and Lacertilia the reverse is the case and the aerated blood passes into the right ventricular chamber."

Now, I willingly admit that my description of the reptilian heart is very general, and in some respects incomplete, and that the diagram given may be somewhat misleading when applied to the Lacertilia and Ophidia (though correct for the Chelonia), for it is scarcely possible to represent the true state

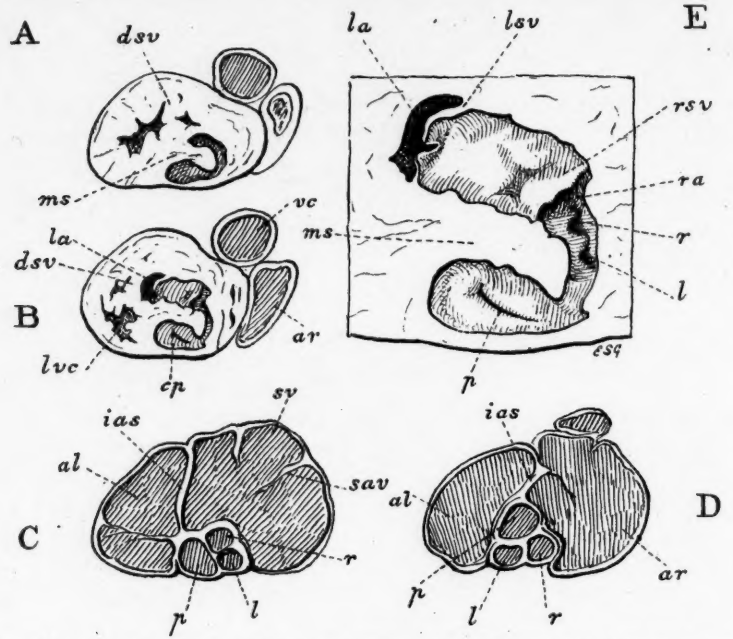


Fig. 2, *A, B, C, D, E.* Python molurus. Transverse sections through the heart, seen from behind, as in figure 1. *E*, portion of figure *B* on a larger scale.

of affairs in a single figure in one plane; but I am quite unable to accept O'Donoghue's interpretation, and am inclined to think that he has misunderstood some fundamental points in the structure of the heart of lizards and snakes.

First of all with regard to the incomplete interventricular septum; O'Donoghue states that in the Ophidia the septum is "attached to the left dorso-lateral side of the ventricle, running from base to apex, and directed towards the right ventro-lateral wall. Thus it runs in a direction entirely different from that of the septum in either Crocodilia or Chelonia," and further, that in the Lacertilia (*Varanus*) it "runs from the left latero-dorsal wall of the

ventricle across towards the right latero-ventral wall, but is decidedly more dorso-ventral in position," dividing the ventricle into "a right lateral, slightly dorsally situated chamber, and a smaller left lateral chamber lying slightly ventrally. The left chamber again gives off only the pulmonary artery, while the right systemo-carotid and left systemic arches both come off from the larger right chamber. Into this chamber also, as in Ophidia, both the auricles open." This description is entirely at variance with my own observations and the recent careful work of Greil on the heart of these reptiles (2), as well as that of older authors. The incomplete muscular septum, although it may shift somewhat laterally towards the posterior apex of the heart, is essentially always a ventral septum developed in relation to the sulcus interventricularis, which passes back from the bulbo-auricular infolding. The septum passes obliquely dorsalwards from the left ventral wall towards the right, and always tends to separate a left dorso-lateral chamber from a right ventro-lateral chamber (cavum pulmonale). This ventro-lateral chamber, leading to the pulmonary artery, is continued up on the right round the free edge of the septum into the more dorsal right region (cavum venosum) of the larger chamber. The true disposition of these structures is shown in the accompanying figures of transverse sections of the heart of Chelone, Varanus, and Python (figs. 1, 2, 3). In these three hearts the ostium of the pulmonary artery is always situated on the right of the base of the muscular septum, which passes between it and the more dorsally situated ostium of the right systemic arch (carotico-systemic). With the help of the medial septal auriculo-ventricular valves, the bulk of the venous blood passes ventrally at auricular systole round the free edge of the septum into the cavum pulmonale; while the bulk of the arterial blood passes across to the right systemic arch. The only important difference between the Chelonia on the one hand, and the Lacertilia and Ophidia on the other, is that, whereas in the former the left arch receives most of its blood from the cavum pulmonale, in the two latter groups by an extra twist upwards of the base of the left systemic arch its ostium comes to lie close to that of the right arch and dorsally to the free edge of the septum, thus receiving more of the arterial blood.

Although O'Donoghue states that in Sphenodon "there is no septum ventriculorum comparable with that of the other Reptilia," I find, like Greil (2), that it exists. The muscular incomplete septum of Sphenodon is small but distinct, and differs in no essential from that of the Lacertilia.

It will be gathered from the description given above that in the anterior region of the ventricle of these reptiles there are two streams of blood crossing each other almost at right angles. The more anterior arterial stream passes from the left region (cavum arteriosum) across to the right arch, and the more posterior stream passes downwards from the right region (cavum venosum) to the cavum pulmonale. Before reaching the base of the various arches the blood passes towards the apex of the heart; and if we follow backwards the three cavities mentioned above (cavum arteriosum, c. venosum, and c. pul-

monale) we find that the cavum arteriosum forms in all the three groups the incipient left ventricle (figs. 1–5), while the cavum venosum and c. pulmonale together belong to the incipient right ventricle. The next important step in the evolution of the sauropsidan heart leading to the four-chambered condition, is the separation of these left dorso-lateral and right ventro-lateral cavities. This appears to be brought about not by the mere fusion of the incomplete muscular septum with the opposite wall, but by the growth from behind forwards of a new muscular septum differentiated from the muscular strands which unite the base of the old septum with the dorsal wall of the ventricle

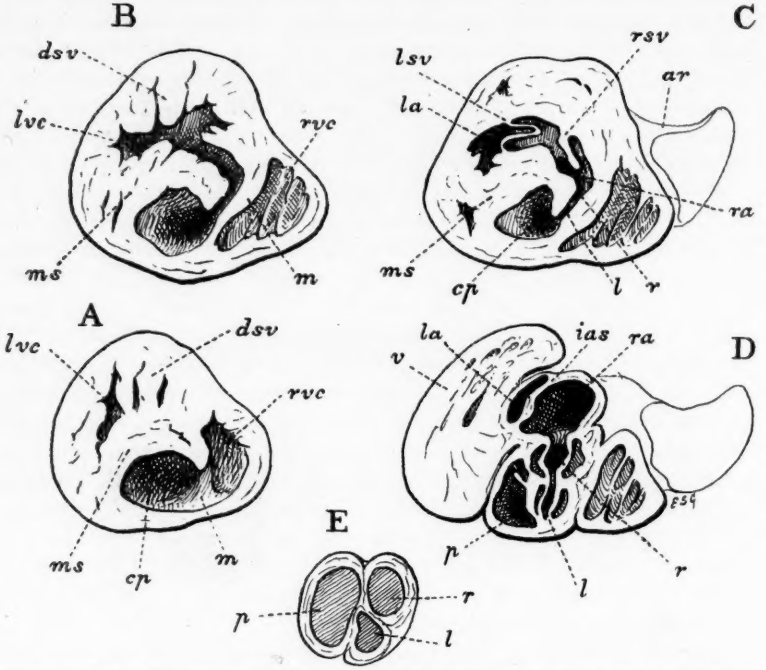


Fig. 3, *A, B, C, D, E.* Varanus sp. Transverse sections through the heart, seen from behind, as in fig. 1.

(figs. 2, 3, 5, Greil(2)). Eventually the completed interventricular septum meets the endothelial cushion thickening the posterior free edge of the interauricular septum, and so a right ventricle corresponding to the cavum arteriosum becomes cut off, from a left ventricle corresponding to the combined c. venosum and c. pulmonale. But before this interventricular septum can be completed it is obviously necessary to ensure that the arterial blood from the left side may reach the ostium of the right carotico-systemic arch. We find, therefore, that in the Crocodilia, where the interventricular septum has joined the interauricular endocardial cushion, the dorso-ventral venous

stream becomes quite cut off from the left to right arterial stream, and for this purpose the base of the right aorta passes over to the left to open more directly into the left ventricle. The formation of the necessary partition has been described in the chick by Greil and Hochstetter (3), and a good account

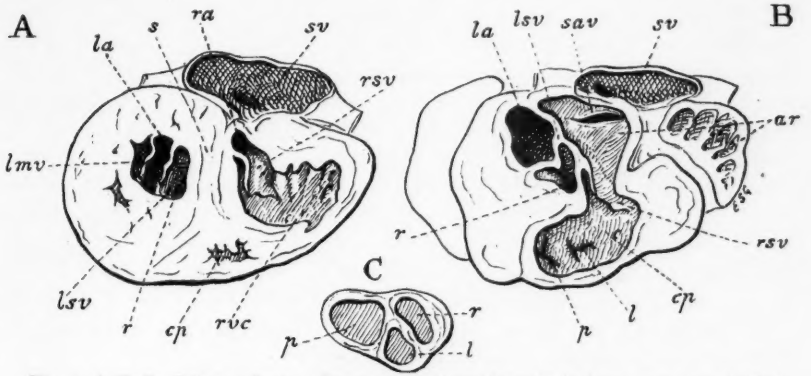


Fig. 4, *A*, *B*, *C*. Caiman sclerops. Transverse sections through the heart, seen from behind, as in fig. 1.

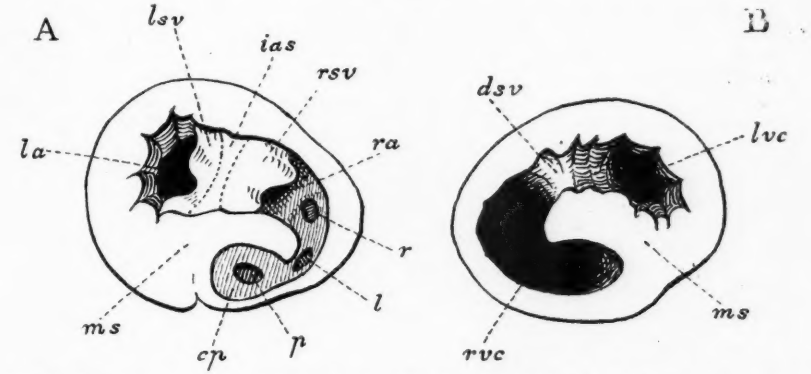


Fig. 5, *A*, *B*. Diagrams of the ventricle of a Reptilian heart (not Crocodilian). *A*, cut transversely and seen from behind; the position of the interauricular septum is indicated by dotted lines. *B*, cut transversely and seen from in front.

of it will be found in Lillie's book (4). It is clear that the essential relations of the right venous and left arterial streams in the single or divided ventricle remain unchanged throughout the Sauropsida, and that there is no foundation for O'Donoghue's statement that they are reversed in the Lacertilia and Ophidia. Indeed these fundamental relations, already foreshadowed in the Pisces and Amphibia, were doubtless definitely established in the common ancestor of all the Amniota, and were determined by the early differentiation of a right venous and a left arterial auricle.

SUMMARY

There is in the ventricle of all living Reptilia a muscular septum attached to the ventral wall, and passing forwards between the left auriculo-ventricular opening and the ostium of the pulmonary artery. Dorsally and to the left of this septum is the cavum arteriosum, while on the right the dorsal cavum venosum passes ventrally round the free edge of the septum to the cavum pulmonale. Muscular strands from the base of the septum to the dorsal wall of the ventricle separate incipient left from incipient right chambers. In the Crocodilia these strands form a wall which together with the septum unite with the endocardial cushion of the interauricular septum, and complete the division of the cavity into a left ventricle corresponding to the cavum arteriosum, and a right ventricle corresponding to the cavum venosum and the c. pulmonale. The left ventricle leads to the right aortic arch, and the right ventricle to the pulmonary artery and the left aortic arch. Whereas in the Chelonia, as in the Crocodilia, the left arch receives most of its blood from the cavum pulmonale, in the Lacertilia and Ophidia it opens more dorsally so as to receive arterial blood as well.

LIST OF REFERENCE LETTERS FOR FIGURES 1, 2, 3, 4, 5

a.l. left auricle; *a.r.* right auricle; *c.p.* cavum pulmonale; *d.s.v.* muscles representing dorsal region of septum ventriculorum; *i.a.s.* interauricular septum; *l.* left aortic arch; *l.a.* left auriculo-ventricular opening; *l.m.v.* left auriculo-ventricular marginal valve; *l.s.v.* left septal (medial) auriculo-ventricular valve; *l.v.c.* left ventricular chamber; *m.* muscle ridge; *m.s.* muscular interventricular incomplete septum; *p.* pulmonary arch; *r.* right aortic arch; *r.a.* right auriculo-ventricular opening; *r.m.v.* right auriculo-ventricular marginal valve; *r.s.v.* right septal (medial) auriculo-ventricular valve; *r.v.c.* right ventricular chamber; *s.* interventricular septum; *s.a.v.* sinu-auricular valve; *s.v.* sinus venosus; *v.* ventricle; *v.c.* vena cava inferior.

LIST OF REFERENCES

(1) Goodrich, E. S. "On the Classification of the Reptilia." *Proc. Royal Soc.* B., vol. lxxxix. 1916.

(2) Greil, A. "Beitr. z. vergl. Anat. u. Entw. des Herzens." *Morph. Jahrb.* vol. xxxi. 1903.

(3) Hochstetter. "Die Entw. des Blutgefässsystems." Hertwig's *Handbuch d. Entw. der Wirbeltiere*, vol. iii. 1906.

(4) Lillie. *The Development of the Chick.*

(5) O'Donoghue, C. H. "The heart of the Leathery Turtle." *Journ. of Anat.* vol. lii. 1918.

THE ACCESSORY PULMONARY LOBE OF THE VENA AZYGOS

By E. PHILIP STIBBE,

Late Demonstrator of Anatomy, Durham University College of Medicine.

The following is the description of an abnormal condition of the Vena Azygos (major) and the right lung, which was observed in an adult male subject in the dissecting room of the Durham University College of Medicine.

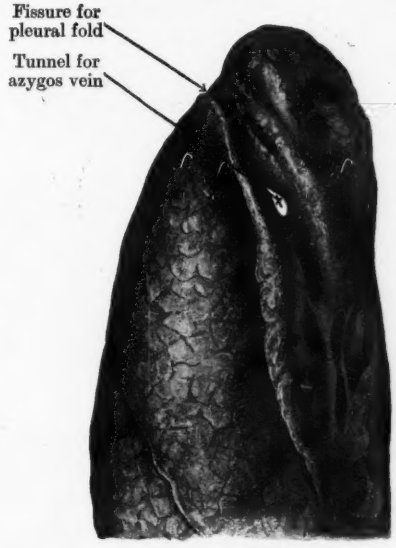


Fig. 1.

Fig. 1 shows the right lung removed from the thorax. The upper lobe is divided by an oblique fissure into two parts. The smaller upper and medial part includes the apex of the lung; the lower part extends from the abnormal fissure to the longitudinal and horizontal fissures respectively posteriorly and anteriorly.

This abnormal fissure closely resembles a normal lung fissure, extending through the lung substance to within an inch of the root of the lung. It is closed by apposition of the surfaces bounding it, except at its deepest part,

where it is oval on section; here when *in situ* it lodged the vena azygos (major). The accessory lobe isolated by the fissure is more or less tongue-shaped and its substance, like that of the rest of the lung, is free from macroscopic pathological change.

Fig. 2 is a view of the interior of the right pleural sac after removal of the right lung. The upper part of the pleural cavity is seen to be divided into two compartments by a dome-like fold which corresponds to, and occupied the fissure seen in fig. 1. The fold is a reduplication of the parietal pleura. Its

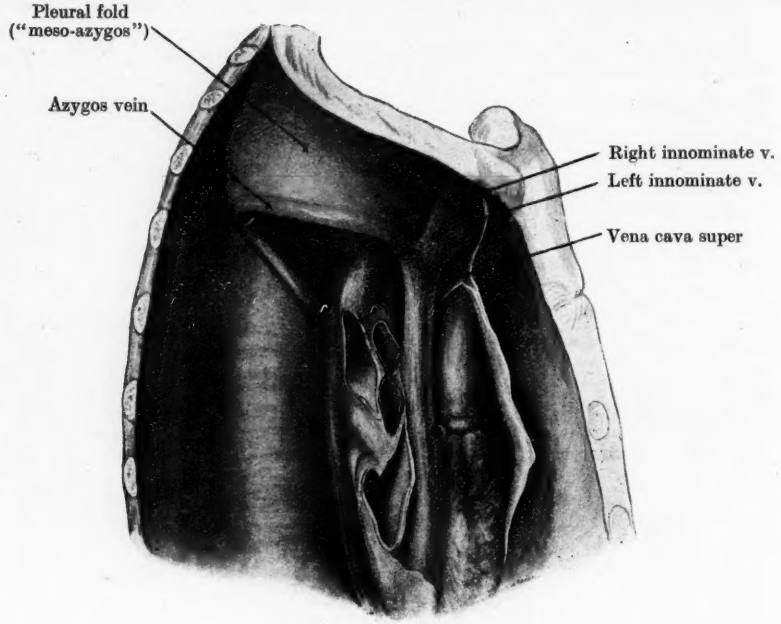


Fig. 2,

convex margin is attached along a line on the thoracic wall; the attachment commences posteriorly at the right side of the fifth thoracic vertebra, passes obliquely upwards across the posterior parts of the intercostal spaces to the middle of the second rib, and then downwards and forwards to the first costal cartilage where it disappears in the parietal pleura of the front of the thorax. The free margin of the fold is concave and contains between its two layers the azygos vein. The pleural fold and azygos vein are related to one another like the mesentery and a portion of the small intestine. By this fold the pleural cavity is divided into an upper and medial diverticulum lodging the accessory lobe of the lung, and a lower compartment for the remainder of the lung. The aperture of communication between the two compartments lodges the pedicle of the accessory lobe.

The *azygos vein* lies behind the oesophagus and just to the right of the midline till it reaches the level of the sixth thoracic vertebra. Here, instead of arching forwards over the root of the lung, it turns backwards and lateralwards, dipping into the substance of the upper lobe, and pulling down with it the pleural fold referred to. Leaving the fissure at its anterior end the vein joins the superior vena cava almost at the point where that vein is formed by the junction of the two innominate veins.

NOMENCLATURE

Extra lobes of the lung have been not infrequently reported. The cases up to 1899 were summarised by Dévé(1), and the subject is discussed in the American Journal by Gillespie, Miller and Baskin(2). Unfortunately the term *azygos lobe* has been applied to a lobe found at the *base* of either lung. This lobe is considerably less common than that under discussion, but anatomists are sufficiently familiar with the term azygos lobe as applied to the basal lobe, to make one desire to avoid altering the name. Moreover, Allen's suggestion of *lobus cavae* for the basal lobe would only apply to cases found on the right side—whereas the left side is also not infrequently found to have an azygos lobe. We propose, therefore, not to interfere with the term azygos lobe, as used at present, but to call the apical lobe cut off by the abnormal azygos vein *the lobe of the azygos vein*, and the fissure *the fissure of the azygos vein*. To those accessory lobes above the root of the lung, which are not cut off by the azygos vein (Nicolle(3), Geddes(4), Grüber(5)) we may apply the term *upper azygos lobe* in contradistinction to the *lower azygos lobe* referred to above; this is a modification of the suggestion of Motti(12).

The lobe and fissure that we are concerned with therefore are the lobe and fissure of the azygos vein.

The following table (p. 310) is a table of twenty-three cases reported to date.

By extracting the common factors of this table we may come to the following general conclusions.

1. *Position of fissure.*

The fissure may occupy one of three positions:

(*a*) More or less horizontal and cutting the outer (lateral) surface of the lung at some point between the apex and a point two inches below the apex.

(*b*) More nearly vertical, and dividing the apex of the lung into lateral halves.

(*c*) Vertical, and cutting off a small tongue-shaped lobe from the inner (mediastinal) surface, the pedicle being attached to the upper margin of the root of the lung.

These we propose to refer to as types *a*, *b*, and *c*. Thus "a lobe of the azygos vein type *c*," would at once convey the meaning of a small lobe on the mediastinal surface of the lung, attached by a pedicle to the root of the lung, and separated by the azygos vein from the upper lobe.

Analysis of the table shows that the type is specified in nineteen cases; the relative frequency of the types is:

Type (*a*). 9 cases out of 19 = 47 %
Type (*b*). 5 „ „ 19 = 26 %
Type (*c*). 5 „ „ 19 = 26 %

This relatively equal distribution of types amongst a small number of cases, suggests that we may expect the fissure to occupy indifferently any position between a point say 1 inch above the root of the lung on the mediastinal surface, to a point say 3 inches below the apex of the lung on the lateral surface.

2. *This lobe and the upper azygos lobe are different structures*—if indeed they are related in any way. This may seem an unnecessary statement, but as indicated above, lobes and fissures have been described closely resembling the lobe and fissure of the azygos vein, yet not connected with the azygos vein, which is normal in these cases.

Geddes (4) found incomplete fissures of types (*a*) and (*b*) in a lung from a case in which the azygos vein was normal. He compared this with his case of true fissure of the azygos vein, and pointed out that in both cases there was an isolated lobe which was supplied by the most medial branch of the trifurcated eparterial bronchus. It must be noted too that a most careful examination was made for any indication of a pathological condition.

Nicolle (3) describes a fissure of type (*a*), in which description no mention is made of the azygos vein; Nicolle, however, was more interested in the pathological (tuberculous) condition of the lung substance in this case than in the anatomical significance of the fissure.

Mayland (6) describes a fissure in position (*c*). In his report he states that being interested in the pathology of the case he had not noticed the position of the azygos vein, and he thinks it likely that this was a case similar to those of Cleland (7) and Chiene (8). (This case has been omitted from the table owing to the uncertainty of its nature.)

Gruber (5) (case No. 7 in table) found a lobe of the azygos vein, type (*a*), with an additional small azygos lobe on the mediastinal surface of the lung. In view, however, of the close approximation of the tabulated cases in essential particulars, we are probably justified in saying that there is no connection between our twenty-three cases and the four cases just mentioned—two of the latter being possibly cases of true lobe of the azygos vein. The other cases only suggest that there is a definite upper azygos lobe, apart from the lobe of the azygos vein.

3. *Course of the azygos vein.* This has been described in only six of the cases. In five of these it is normal as high as the fifth thoracic vertebra (upper border of the root of the lung), at which level it deviates backwards and to the right. The sixth case (Wrisberg (9)) gives the vein a normal course to the third intercostal space; this after all, is only slightly above the level of the fifth vertebra, and does not differentiate Wrisberg's case from the others.

Dévé(1) detects a *slight* deviation of the vein to the right in its whole length. According to him the normal azygos vein occupies the mid-line *exactly*, in its course from the aortic opening to the fifth thoracic vertebra; what we have therefore rather loosely called a normal vein, is only normal if it lies *in front* of the bodies of the vertebrae, not on their right side—a point of some importance because Dévé(1) considers this deviation of the vein to be the primary cause of the abnormality. We doubt if many anatomists would agree with this strict interpretation of the position of a normal azygos vein; in any case it is at the fifth thoracic vertebra that the obvious and significant deviation begins.

4. *Level of junction of azygos vein with vena cava superior.* This is mentioned in ten cases, and is in nine cases at the junction of the two innominate veins, that is at the commencement of the superior vena cava. This may be interpreted as an obliteration of that part of the anterior cardinal vein which normally forms part of the superior vena cava, the latter in such a case being developed entirely from duct of Cuvier (common cardinal vein). This in turn would accord well with the view that the descent of the heart has been interfered with by the lung-bud coming into contact with the azygos vein. (See below.)

5. *Depth of fissure.* This is defined in twelve cases, and there is some diversity, but the fissure seems usually to approximate to a primary lung fissure. In cases 3, 9 and 20 the vein rests upon the eparterial bronchus or its medial branch. In other cases (6, 14, 21, 22) a small quantity of lung tissue separates the vein from the bronchus.

In the present case there is about 1 inch of lung tissue between the deepest part of the fissure and the bronchus. Geddes (case 21), Gruber (case 9) and Dévé(1) figure a distorted ∽-shaped medial (first) branch of the eparterial bronchus, the vein lying in the upward concavity.

CAUSATION OF THE ABNORMALITY

The immediate cause of the abnormality is an alteration in the relationship of the developing lung to the developing azygos vein.

In models of 4 mm. embryos it is seen that the descent of the heart from its cervical to its thoracic position has drawn forwards and downwards the anterior part of the posterior cardinal vein (vertebral vein, Gegenbauer(10); prevertebral plexus, Sabin(11)). The lung bud at this time has just commenced to bifurcate; subsequently (5–7 mm. embryos) the apical lobe of the right lung is seen to grow from the right bronchus, and, to get to its normal position this future apex of the right lung must pass under (caudally to) the arch of the future azygos vein. In the cases under consideration the lung bud has failed to clear the venous arch; the vein is a relatively tough structure and "instead of slipping behind the pleura and lung, has dragged down a fold of the former, and deeply notched the latter" (Cleland(7)).

Table of reported cases of the Lobe and Fissure of the Azygos Vein.

Serial Number	Date of Report	Reported by	Age of Subject	Position of Fissure	Depth of fissure	Azygos vein deviates at level of	Termination of azygos vein	Remarks
1	1778	Wrisberg[9]	3	Nearly horizontal, cutting outer surface of lung well below apex (see figure)	—	Third intercostal space	So high that it is difficult to say whether it is in rt. vena innominata or in vena cava superior	Vena azygos minor drained into left innominate vein and fissured left lung in the same way as the right
2	1861	Rokitanski[14]	—	—	—	—	—	Compares fold with supernumerary peritoneal folds
3	1862	Bouchard[15]	$2\frac{4}{12}$	Horizontal fissure dividing upper lobe into two	Reaches as far as the root of the lung like the other fissures	—	—	Fold of pleura serves as a mesentery for vena azygos major
4	1869	Chiene[8]	50	Figured close to apex of lung	—	Fifth thoracic vertebra	—	Size of accessory lobe $3\frac{1}{4}''$ long, $2''$ broad, $1''$ thickness at pedicle
5	1870	Cleland[7]	—	To medial side of apex of lung (by inference)	A deep notch	—	—	—
6	1870	Gruber 1[5]	Adult	—	To within $\frac{1}{4}''$ of the right upper bronchus	—	At junction of two innominate veins	—
7	1870	Gruber 2[5]	—	Cuts outer surface of lung below apex	—	—	At junction of two innominate veins	Additional accessory lobe on medial surface of lung
8	1874	Collins[17]	—	—	—	—	—	Reference not accessible
9	1880	Gruber 3[16]	—	Cuts outer surface of lung, well below apex	To root of lung	—	At junction of two innominate veins	Accessory lobe supplied by upper (medial) branch of upper (eparterial) bronchus

10	1882	Allen 1[18]	Foetus	Oblique sulcus which indents back of apex of lung	—	—	Higher than normal. Vena cava elongated	Allen suggests that this lobe—not the lobe sometimes found at base of lung—should be called azygos lobe. The lobe at the base of the lung, he would call *lobus cavae*
11	1882	,, 2[18]	Adult	Ditto	—	—	—	
12		,, 3[18]	,,	Ditto	—	—	—	
13	1887	Sperino[19]	—	Stated by Dévé to be same as No. 5	—	—	—	Reference not accessible
14	1893	Josselin de Jong[22]	63	Cuts outer surface of lung below apex	To within 3 cm. of hilus of lung	—	—	—
15	1893	Motti[12]	—	Cuts outer surface of lung below apex	—	—	—	Accessory lobe 6 cm. by 2 cm. suggests *superior azygos lobe*
16	1897	Maüsert[21]	—	—	—	—	—	Reference not accessible
17	1898	Matthews	36	Vertical, cutting outer surface $\frac{1}{2}''$ below apex	Constricted lung tissue between vein and root of lung	—	Figured in usual position—behind 2nd cost. cartilage	Lobe $2\frac{1}{2}''$ long. Pedicle $1''$ by $1\frac{3}{8}$
18		Dévé 1[1]	Foetus $\frac{3}{12}$	Cuts outer surface of lung well below apex	Small quantity of lung tissue separates bottom of fissure from bronchus	Upper border of root of lung	At junction of two innominate veins	Dévé describes the accessory lobe as being supplied by the medial of three branches of eparterial bronchus. This branch is contorted to Ω-shape by pressure of azygos vein (cf. No. 20)
19		,, 2[1]	34	Crosses apex of lung		Ditto	Ditto	
20	1899	,, 3[1]	$\frac{5}{12}$	Confined to medial surface of lung, well below apex		Ditto	Ditto	
21	1910	Geddes[4]	—	Confined to medial surface of lung, well below apex	Reaches upper bronchus	—	At junction of two innominate veins	Supplied by medial of three branches of eparterial bronchus with distortion exactly as in (19)
22	1915	Holtby[22]	Adult	Confined to medial surface of lung, near apex	Does not quite reach root of lung	—	At junction of two innominate veins	—
23	1916	Stibbe	Adult	Cuts outer surface of lung $1\frac{1}{2}''$ below apex	Separated from root of lung by $1''$ of lung tissue	Sixth thoracic vertebra	At junction of two innominate veins	—

The immediate cause of this must be either

(1) A primary abnormal position of the posterior cardinal vein and common cardinal vein, or

(2) A fault in the development of the lung.

Between these two possibilities we will not presume to decide—it becomes now a matter for speculation. The following suggestions, however, are interesting:

Cleland (7) suggests that "there has been at a very early period, a slight adhesion of the lung to the thoracic wall, or much less probably an undue curvature of the embryo, so that the vena azygos," etc., *vide* above.

Dévé, however, finds it difficult to imagine an adhesion of the lung to the parietes at this early stage; or, given such an adhesion of the very minute lung-bud, it is difficult to think its only effect is to produce this single abnormality. Further, a concavity of the embryo to the right would produce the requisite deviation of the azygos vein, but Wrisberg's case showed the same abnormality on the left side (vena azygos minor or left superior intercostal vein, producing fissure of left upper lobe); abnormal curvature would not affect both sides in the same way.

Motti (12) found that the distance from the bifurcation of the trachea to the azygos vein was definitely diminished in his case, being only 8–10 mm., instead of the normal 12 mm.; Sappey (13) gives 15–18 mm. as the length of the right bronchus to the hilus of the lung. He therefore considers that the lung bud does not grow out far enough.

Matthews (23) is also inclined to attribute the abnormality to the lung in the first instance. He points out that the lung bud has to grow downwards and outwards to reach the space external to the venous arch, and that a slightly higher point of outgrowth of the lung bud would cause the upper lobe to impinge on the vein instead of clearing it. It is not necessary indeed for the position of the lung-bud to be higher than usual—a slight alteration of the time-relationship, the lung outgrowth being slightly delayed, or the descent of the heart slightly advanced, would cause the same condition. Matthews further shows that the greater portion of the lung would still reach the "external cavity," as the direction of the growing bronchus is downwards —only a small portion of the apex would, therefore, be finally "held up." In the type (*c*) cases the apex of the adult lung would originally have been lower than (caudal to) the part forming the abnormal lobe.

Dévé's view (1) is that the vein is primarily deviated, and is based partly on his definition of the normal position of the lower part of the azygos vein (see above).

He finds difficulty too in conceiving that the form of the lung should determine the position of the vein; the form of the adult lung is certainly determined by the pressure of the surrounding structures—not *vice versa*.

We think the question could only be decided by the detection of the abnormality in a 4–5 mm. foetus—a somewhat unlikely event.

I am indebted to Professor Howden for allowing me to report this specimen, and for help in the matter of description and references; also to Professor Keith for advice and help.

The drawings are the work of Mr S. A. Sewell.

SUMMARY

1. Three varieties of supernumerary lobes of the lung are known:

(*a*) Lobe of the azygos vein.

(*b*) Upper azygos lobe—not associated with abnormality of the azygos vein.

(*c*) Lower azygos lobe—previously called azygos lobe.

Of these varieties the first appears to be the commonest, and is very much commoner than the second.

2. The present case is one of the first variation; a lobe and fissure of the azygos vein.

3. Analysis of twenty-three cases of this abnormality shows the following general points:

(*a*) The fissure may cut the lung at any level, from an oblique plane cutting the outer surface of the lung 2 inches below the apex, to a vertical plane cutting off a small tongue-shaped lobe from the mediastinal surface. Between these extremes is an intermediate type passing approximately through the apex of the lung.

(*b*) The first type is the commonest, but a larger number of cases may show about equal numbers of each.

(*c*) The azygos vein pursues a normal course from the aortic opening to the fifth thoracic vertebra, where it turns back and to the right to sink into the azygos fissure.

(*d*) The azygos vein empties into the junction of the two innominate veins—commencement of superior vena cava.

(*e*) The fissure approaches the root of the lung, and in some cases actually rests on the exposed medial branch of the eparterial bronchus.

4. The cause of this abnormality is a failure of the lung bud to clear the venous arch produced by the forward and downward traction on the anterior end of the posterior cardinal vein. It is not known whether the lung fails to extend so far as usual to the right, or whether the vein is already deviated to the right side so that a normally extending lung bud fails to get entirely beyond the vein. If the primary departure from the normal is the deviation to the right of the vein, the cause of this has still to be sought.

REFERENCES

(1) Dévé. *Bull. et mem. Soc. Anat.*, LXXIV. Paris, 1899.
(2) Gillespie, Miller and Baskin. *Anat. Record*, vol. II. 1917.
(3) Nicolle. *Bull. et mem. Soc. Anat.*, Paris, 1887.
(4) Geddes. *Journ. of Anat. and Phys.*, vol. XLV. 1910.
(5) Gruber. *Bull. Sc. Sciences*, St Petersburg, T. IV. 1870.
(6) Mayland. *Journ. of Anat. and Phys.* vol. XX. 1886.
(7) Cleland. *Ibid.* vol. IV. 1870.
(8) Chiene. *Ibid.* vol. IV. 1870.
(9) Wrisberg. *Obs. anat. vena azyga duplici aliisque hujus venae varietatibus*, Gottingen, 1778.
(10) Gegenbauer. *Elements of Comparative Anatomy*, Macmillan.
(11) Prentiss and Arey. *Text-book of Embryology*, Saunders.
(12) Motti. *Giom. Internat. Scienz. Mediche*, 1893.
(13) Sappey. In Dévé's paper—ref. No. 1.
(14) Rokitanski. *Traité d'anatomie pathologique*, 1861.
(15) Bouchard. *Bull. et mem. Soc. Anat.* Paris, 1862.
(16) Gruber. *Arch. Virchow*, 1880.
(17) Collins. *Journ. of Anat. and Phys.* 1874.
(18) Allen. *Ibid.* 1882.
(19) Sperino. *Giorn. della R. Acad. di Med. di Torino*, 1887.
(20) de Jong. *Ned. Tijdsch. voor geneeskunde*, 1893.
(21) Maüsert. *Giorn. della R. Acad. di Med. di Torino*, 1897.
(22) Holtby. *Journ. of Anat. and Phys.* vol. XLIX. 1915.
(23) Matthews. *Ibid.* N.S. vol. XII. 1898.

THE PRIMORDIAL CRANIUM OF *MINIOPTERUS SCHREIBERSI* AT THE 17 MILLIMETRE TOTAL LENGTH STAGE[1]

By Professor FAWCETT, M.D.,

University of Bristol

The embryo from which the models about to be described were made I owe to the kindness of Prof. J. P. Hill. It had I think been fixed in picric acid, a fact which gave me much trouble afterwards. It was in a fairly advanced state of ossification which increased the difficulties of making the reconstructions although in some respects it added to their interest.

Miniopterus schreibersi belongs to one of the two genera of the miniopterine division of the family Vespertilionidae and according to Flower and Lydekker (1) is the best-known of the four species of Miniopterus. It is very widely distributed, being found almost everywhere throughout the tropical and warmer temperate regions of the eastern hemisphere; specimens from Germany, Madagascar, Japan and Australia differing in no appreciable respect from one another.

The head of the animal before sectioning is of a comparatively simple type more especially as concerns the nose which is quite free from the elaborate external nasal appendages of the Rhinolophidae, but when one examines the deeper lying chondrocranium one is at once struck with the great elaboration and complexity of the anterior parts of the nasal capsule. But as will be seen later they are mere elaborations of what seems to be a common plan in the construction of the anterior region of the nasal capsule, and in the solution of this question the modelling of older stages such as this is essential.

The head of this embryo was cut into serial sections of 15μ thickness and the model was made at an enlargement of 66·6 diameters in order to provide wax plates of one millimetre in thickness. As some cartilaginous parts were in a comparatively advanced state of ossification considerable difficulty was experienced in determining how much was originally to be assigned to cartilage and how much to perichondrial ossification—and the limits of ossification were not at all easy to determine as regards the auditory capsule, for the main reason that owing to the whole of the picric acid not having been thoroughly washed out of the tissues, false staining resulted, cartilage for example staining yellow instead of blue with Mallory's stain, and the bones doing the same

[1] The expenses of this research were defrayed by a grant from the University of Bristol Colston Research Society.

thing in several sections. Several slides of sections had in fact to be restained, and the result of restaining with Mallory's stain is—at all events in my hands—very uncertain. Then, too, especially in the thin-walled cochlear capsule the cartilage before ossification seems to undergo a sort of fibrous degeneration and this staining in a somewhat tricky manner added to the difficulties[1].

It will be seen as the parts are described in detail that whilst there are special modifications in certain parts the primordial cranium of Miniopterus follows pretty closely that of other mammals, and it certainly is of great interest.

Before entering into these details a short account of the conditions holding good for the adult cranium may be not out of place. According to Weber(2) on the skull in Microchiroptera the facial part is sometimes so shortened "dass die Gesichtsknocken darunter litten." "Ihr Hirnschädel ist gleichfalls verkürzt, dabei aber verbreitert und abgerundet, mit Demarkation der darunterliegenden cerebellaren, cerebralen und olfaktorischen Hirnabteilung. Abgesehen von der Tatsache, das die Nähte der Schädelknocken, namentlich aber die Gesichts, bei Microchiroptera, früh verschmelzen, influenzierte auf deren Schädel unzweifelhaft die Gewohnheit, Insekten im Fluge zu haschen. Dies forderte eine weite Mundspalte und daneben ein kräftiges Gebiss, dementsprechend starke Ausbildung des Musc. temporalis und der mm. pterygoidei.... Den grossen Pterygoidmuskeln entsprechen nach hinten ausgedehnte Pterygoidei. Die Fossae pterygoideae dagegen sind klein....Das Foramen lacrimale liegt facial....Die Wand der Schädelhöhle wird namentlich durch die grossen Parietalia gebildet. Orbito- und Alisphenoid können teilweise häutig bleiben, so dass das Foramen opticum alsdann der knöchernen Umrandung entbehrt. Das Petrosum....bei Microchiroptera ist das Knochengewebe so sparsam, dass das knöcherne Labyrinth mit seinen halbzirkelförmigen Kanälen und mit der Cochlea deutlich zu Tage tritt. Letztere hat derartige Ausdehnung, dass dem Basioccipitale zwischen den beiderseitigen Cochleae nur beschränkter Raum erübrigt. Bei Megachiroptera ist die Trommelhöhle nur häutig geschlossen, das Tympanicum schmal ringförmig, lose. Bei Microchiroptera soll es dagegen zu einer Bulla aufgeblasen sein die aber stets an die ursprüngliche Ringform erinnert und wohl nie die ganze Trommelhöhle umwandent, auch liefert es keinen knöchernen äusseren Gehörgang. E. Blanchard und Maisonneuve erkannten jedoch bereits, dass die Bulla selbständig entsteht und erst sekundär mit dem Tympanicum verschmilzt, das, wenn auch verbreitert, seine Ringform bewahrt....Der Gaumen der Microchiroptera aber liegt entweder in gewohnter Weise in der Flucht der Schädelachse oder er ist nach aufwärts gebogen. Begegnen sich die Intermaxillaria nicht in der Medianlinie ist der Gaumen nach vorn offen; er wird hier durch Knorpel ergänzt der aber auch fehlen kann (Rhinolophidae Grosser). Auch die Ausdehnung des Gaumens nach hinten über die Zahnreihe hinaus ist eine verschiedene.

[1] I have since found that if the aniline blue of the stain be thoroughly removed by alcohol, restaining is simple and satisfactory.

Die Nasenhöhle erfuhr Reduktion infolge des Gesichtsschädels, jedoch in verschiedenem Grade. Bei sämtlichen erlitt das Nasoturbinale Rückgang, der fast zum Schwunde führen kann. Die Ethmoturbinalia sind gering an Zahl, aber noch in zwei Reihen angeordnet und gewunden (Vespertilionidae z. B.); sie scheinen aber bei Rückbildung der Intermaxillaria einfach zu werden und sich auf eine Reihe zu beschränken (H. Allen, Grosser). Dieser Rückschritt kann sich auch auf das Maxilloturbinale ausdehnen.

Am Unterkiefer ist der aufsteigende Ast meist niedrig, der Processus coronoideus meist breit für den Ansatz des starken Musc. temporalis, der Processus angularis sehr verschieden stark entwickelt; der Condylus mandibulae bei den Megachiroptera merklich verbreitert."

THE PRIMORDIAL NEURAL CRANIUM

This, in accordance with the plan which I have adopted in previous communications, is divisible into the following parts:

1. A central stem, to which are appended, at more or less constant positions,
2. Appendages to the central stem,
3. Lateral structures,
4. Commissures binding the central stem and the appendages together,
5. Commissures binding the lateral structures together,
6. Dorsal structures, viz. those which lie dorsal to the encephalon and form a cartilaginous roof to the cavum cranii.

1. The Central Stem (Pls. XIII, XIV).

The central stem stretches from the anterior margin of the foramen magnum to the top of the nose. It consists of the following parts, viz. from behind forwards: a *pars chordalis*, a *pars trabecularis* and a *pars interorbito-nasalis*. (It has been shown elsewhere on what grounds this mode of description is based.) With the exception of that part which is included within the nasal capsule, the central stem tends to be flattened from above downwards, the intra-nasal part being flattened from side to side.

Detailed Description of the Central Stem.

The pars chordalis is to a large extent ossified to form the basi-occipital segment of the occipital bone, but anteriorly and postero-laterally it is still cartilaginous. In general form, as seen either from above or below, it is triangular in shape with the angles blunted.

Each postero-lateral or basal angle is delimitable by an imaginary line drawn through the anterior margin of the hypoglossal canal of its side. At this imaginary line each is continuous without histological difference into the exoccipital cartilage and from the anterior side of each basal angle a commissure —the chordo-cochlear commissure (Pls. XIII, XIV, XVII)—connects the pars chordalis with the hinder part of the cochlear capsule. This chordo-cochlear

commissure shows some sign of ossification which is continuous with similar ossification of the cochlear capsule. The anterior basal angle is cartilaginous and fused without histological differentiation with the back of the pars trabecularis, only the site of emergence of the chorda dorsalis behind the crista transversa of the pars trabecularis giving any hint as to the anterior end of the pars chordalis. There are three borders, viz. a posterior and two lateral. The posterior border is concave backwards and forms the anterior margin of the foramen magnum. At its middle it is deeply indented forming the so-called *incisura anterior*. The indentation is caused by the dens of the axis vertebra. The anterior border towards its lateral extremity enters into the formation of the corresponding occipital condyle. Each lateral border is thin and for the most part consists of bone. It is separated from the cochlear capsule by a fissure which is the basi-cochlear fissure. This fissure extends from the chordo-cochlear commissure behind to the anterior trabeculo-cochlear commissure in front. It is therefore in direct continuity with the carotid canal. This confluence seems to result from the disappearance of a cartilaginous posterior trabeculo-cochlear commissure, fibrous traces of which persist. The upper or caval surface of the pars chordalis is triangular in form and very slightly concave from side to side (Pl. XIII). It is wide in its posterior half but narrow anteriorly where cartilaginous. Its narrowness recalls that seen in the corresponding region of the cat's cranium and is clearly due to the large size of the cochlear capsules. The inferior surface (Pl. XIV) is convex from side to side, a fact marked by a keel-like antero-posterior ridge especially in its anterior half. The posterior half is much more gently concave from side to side.

There is no indication of any histological line of demarcation between the pars chordalis and the pars trabecularis, but it is not difficult to surmise where such demarcation ought to be.

The pars trabecularis (Pls. XIII, XIV) is readily recognised in the main by its being hollowed on its upper surface to lodge the pituitary body. It is of great length from behind forwards, recalling the condition observed in *Microtus amphibius*. Part of its apparent length is due to the failure of the post-optic limb of the ala orbitalis to meet the central stem as in the case of Microtus. Viewed from above it has a somewhat cruciform appearance (Pl. XIII), the hind limb of the cross stretching backwards to fuse with the anterior end of the pars chordalis and being interrupted on its caval surface by a prominent *crista transversa* which bounds the pituitary fossa posteriorly. This hind limb is not ossified. The forelimb of the cross is ossified in its caudal half, but in front of this entirely cartilaginous. The lateral limbs of the cross represent the processus alares and each is ossified in direct continuity medially with the centre of the cross which is ossified to form a single mass, the post-sphenoidal centre of ossification. At its outer end the processus alaris is continued anteriorly and posteriorly as cartilage, the posterior continuation is the anterior trabeculo-cochlear commissure which is directly fused with the cochlear capsule, whilst the anterior continuation is a somewhat small ala temporalis,

which is notched on its lateral margin by the mandibular division of the fifth cranial nerve. It is not quite certain whether at an earlier stage the ala temporalis was formed independently of the processus alaris + ant. trabeculo-cochlear commissure but there does seem to be a junctional region at which the cartilage is of a younger type. Additionally it is bounded, laterally and anteriorly by the ossified membranous alisphenoid and along the anterior half of its medial edge it is in contact with the upper part of the pterygoid bone, which also supports it from below. The central part or body of the cross is of considerable size, flattened on its under aspect, but hollowed out cavally to lodge the pituitary body.

The pars interorbito-nasalis is of great length, longer in fact than the combined pars chordalis and pars trabecularis. In its posterior part it is flattened from above downwards and is directly fused with the ala hypochiasmata and with the pre-optic limb of the ala orbitalis on each side and this fusion greatly increases the apparent width of the interorbital part of this segment of the central stem. Its real width may be ascertained in the interval between the alae orbitales behind and the hinder part of the nasal capsule in front. The nasal part of the pars interorbito-nasalis is the nasal septum which is deep posteriorly at the junction of the anterior two-thirds with the posterior third, and comparatively low in height anteriorly. As seen from the side it is almost triangular in outline, the base of the triangle being backwards towards the cavum cranii where it forms the crista galli whose free edge directed towards the cavum cranii is almost at right angles to the rest of the septum and whose dorsal angle is prolonged back under the interfrontal suture in the form of a long spur (Pl. XV). The further description of this region will be undertaken with that of the nasal capsule.

2. Structures Appended to each side of the Central Stem (Pls. XIII, XIV).

These structures which are paired are from behind forwards:

(*a*) The exoccipital cartilage.
(*b*) The auditory capsule.
(*c*) The ala temporalis.
(*d*) The ala orbitalis.
(*e*) The lateral nasal capsule.

(*a*) *The Exoccipital Cartilage* (Pls. XIII, XIV, XVII).

Each exoccipital cartilage may be regarded as the postero-lateral continuation of the corresponding basal angle of the pars chordalis. In this instance each has commenced to ossify, a circumstance which for some reasons somewhat complicates matters and for others makes simple what might be somewhat difficult, more especially as the supraoccipital cartilage is almost wholly ossified. The site of commencement of the exoccipital cartilage is sufficiently indicated by a line drawn across the anterior edge of the hypoglossal canal. From this it passes backwards and outwards at first with a curved direction

concave towards the foramen magnum of which it forms the anterior half of the lateral boundary. It presents to view two surfaces, viz. a caval directed upwards and medialwards towards the cavum cranii, and an extra-caval or inferior surface which is directed towards the neck. The margins may be described as median and lateral.

We will examine the surfaces first.

The *caval* or *superior surface* (Pls. XIII, XVII) is of considerable size. At its commencement in front it is at first narrow from side to side and is notched by the hypoglossal canal which is completed in front by the pars chordalis. Speaking of the exoccipital as a separate entity this part appears to be connected with the pars chordalis by two prong-like projections which embrace between them the hypoglossal or twelfth cranial nerve here in two bundles, and the upper prong is connected with the pars cochlearis of the auditory capsule, by means of a commissure which is really the somewhat broad chordo-cochlear commissure which has extended beyond its usual limits to reach the exoccipital cartilage. The lower prong is the deeper of the two and helps to form at its under border the anterior part of the exoccipital condyle. Behind the site of off-springing of these prong-like boundaries of the hypoglossal canals the caval surface of the exoccipital cartilage increases in size mainly owing to its being prolonged under the canalicular part of the auditory capsule as the *lamina alaris*, forming a large grooved area here which lodges the lower part of the lateral sinus. This groove is overhung by the very prominent *crus commune* of the confluent anterior and posterior semicircular canals and by its lateral edge this part of the caval surface of the exoccipital cartilage is confluent with the pars canalicularis of the auditory capsule. Traced in a forward direction the grooved part of the caval surface of the lamina alaris runs out as the upper surface of a tolerably well-marked *processus paracondyloideus* and a large foramen, the foramen jugulare intervenes between this and the overlying auditory capsule and is bounded medio-anteriorly by the chordo-cochlear commissure. This foramen jugulare is not continued backwards as a fissura supra-alaris as is the case in other animals described. This may however be a difference due to greater age. Behind the region of the auditory capsule the caval surface of the exoccipital cartilage becomes narrower and merges insensibly into that of the now ossified supraoccipital.

The nuchal or inferior surface of the exoccipital cartilage (Pl. XIV) resembles in general outline the caval surface, but differs in many details. It is concave laterally where it is continuous with the inferior surface of the processus paracondyloideus. It is convex towards its medial margin where it takes part in the formation of the occipital condyle.

As this surface of the exoccipital cartilage is traced backwards beyond the limits of the ossific centre mentioned it ultimately blends with the corresponding surface of the supraoccipital cartilage.

The *processus paracondyloideus* (Pl. XIV) is of considerable size and placed under the anterior end of the posterior semicircular canal with whose under

surface it is directly confluent although a deep gap intervenes between the two, a gap which is however only visible from without (Pl. XV, text-fig. 1). This gap is the representative of the exoccipito-capsular fissure of other animals in which it is present.

The margins or borders of the exoccipital cartilage are median and lateral.

The *lateral* margin (Pls. XIII, XIV) when traced from before backwards, consists of first a part which, belonging to the upper margin of the hypoglossal canal, is fused with the chordo-cochlear commissure and through that with the pars cochlearis of the auditory capsule; secondly a free concave part which forms the hinder and inferior margin of the foramen jugulare; beyond this it may be perhaps best described as being double-lipped, having a median lip fused with the pars canalicularis (posterior semi-circular canal) and crus commune of the auditory capsule along the whole length of its postero-inferior aspect, and a lateral lip which is free and extending back from the processus paracondyloideus forms the lower lip of the mouth of entrance to the representative of the exoccipito-capsular fissure (fig. 1).

The *median* boundary or border extends backwards first as the occipital condyle, then becomes suddenly prominent and sharp, due to the formation of a cap of articular cartilage here, after which it becomes less prominent and it ends finally by becoming confluent with the lower margin of the ossified supraoccipital (Pl. XIV). It forms the anterior half of the lateral margin of the foramen magnum.

(*b*) *The Auditory Capsule* (Pls. XIII, XIV, XV, XVI, XVII).

The auditory capsule is remarkable in several respects---amongst which and perhaps most noticeable are the great prominences of its semicircular canals and the almost complete isolation of the anterior one. The lateral semicircular canal too forms a very marked prominence on the lateral aspect of the capsule (Pl. XV). The fossa musculi stapedii is of enormous size (Pl. XIV). The capsule is directly fused to a large part of the exoccipital cartilage, but the cochlear part of the capsule which is of large size is only in the most meagre fashion fused to the central stem.

The auditory capsule is divisible into the two following parts, viz. a hinder, the *pars canalicularis*, and an anterior, the *pars cochlearis* (Pl. XVII).

Of these two the hinder or pars canalicularis is the larger and as seen from without and below appears to be placed almost at right angles with the pars cochlearis. This rectangular form of the capsule as seen from the infero-lateral aspect is very largely due to the great prominence of the lateral semicircular canal.

The capsule is moored to surrounding parts in the following way. Above, to the cartilaginous brim of the cranium through the *lamina parietalis* (Pl. XV), which starts from the fore-end of the anterior semicircular canal, passes upwards to separate the supraoccipito-capsular fissure from the spheno-parietal fontanelle. Next it is moored to the opercular process of the supraoccipital

cartilage by a supraoccipito-capsular commissure which attaches itself to the hinder end of the posterior semicircular canal just before that joins the crus commune. This commissure separates the supraoccipito-capsular fissure from the exoccipito-capsular fissure which is really open for a short distance here to transmit a small vein to the exterior. The pars canalicularis is fused to the whole median lip of the lateral border of the exoccipital by what may be called an exoccipito-capsular commissure which takes a large part in the formation of the sulcus which lodges the *sinus venosus lateralis* (fig. 1).

The pars cochlearis is remarkably free from attachment to neighbouring parts of the chondrocranium. It is fused to the postero-lateral angle of the pars chordalis of the central stem by a comparatively small commissure, the *chordo-cochlear commissure* (Pls. XIII, XIV, XVII), which separates the jugular foramen posteriorly from the basi-cochlear fissure anteriorly. It is fused directly to the pars trabecularis by the anterior trabeculo-cochlear commissure which is of small size, but at this stage there is no posterior trabeculo-cochlear commissure, that having apparently disappeared by absorption, and the carotid foramen is thus confluent with the basi-cochlear fissure. The detailed description of the auditory capsule may now be entered upon and the pars canalicularis will be dealt with first.

The *pars canalicularis* (Pls. XIII, XIV, XV, XVI, XVII) is as generally in mammals of the form of a three-sided pyramid whose base is placed forwards. Its surfaces may be described as lateral, supero-mesial or caval, infero-mesial and basal or lateral, four in all.

The lateral surface (Pls. XV, XVI) is wholly extra-caval and roughly triangular in form with its apex (cupola) directed backwards and partly hidden from view externally by the opercular process of the supraoccipital cartilage. It presents to view three borders which are, one superior, one inferior, and one basal.

The superior border or *prominentia semicircularis anterior* (Pl. XV), commences behind at the cupola and arches upwards and forwards then downwards and forwards to become confluent with the upper end of the basal border. At the site of confluence a swelling is found which is the commencement of the *prominentia utriculo-ampullaris superior* (Pl. XVII). If we regard the superior border as the anterior-semicircular canal then we have here one of the characteristic features of the group to which Miniopterus belongs, for this anterior semicircular canal is, save at its anterior and posterior extremities, absolutely isolated from the rest of the pars canalicularis, a large vacuity separating the two, and this large vacuity takes very largely the place of the fossa subarcuata anterior, and it owes its existence to the very large size of the floccular segment of the cerebellum (fig. 1). In *Microtus amphibius* which I described in Vol. LI of this Journal at the 17·5 total length stage and which was almost as far advanced in development as this specimen of Miniopterus there is a very deep fossa subarcuata anterior whose floor is perforated to the exterior by a small foramen, but the flocculus does not rest in the fossa as in

Miniopterus, and the small foramen just mentioned is in striking contrast to the relatively enormous opening seen in Miniopterus. It may then be safely concluded that this vacuity which largely replaces the fossa subarcuata anterior is due to the large size of the flocculus of Miniopterus, and that this large sized flocculus is correlated with the habits of the bat.

The *inferior border* commences at the cupola posteriorly and passes downwards and forwards to become confluent with the lower end of the basal border. As it is caused by the posterior semicircular canal it may be called the *prominentia semicircularis posterior* (Pl. XV). It separates the lateral from the infero-mesial surface and at its anterior extremity enlarges to form the commencement of the *prominentia utriculo-ampullaris posterior* (fig. 2). Between it and the underlying lateral margin of the exoccipital cartilage there is a deep fissure which is only at its hindmost part confluent with the cavum cranii and is the representative of the exoccipito-capsular fissure of those animals in which it exists. This fissure is shallow at its anterior end owing to the fact that the prominentia semicircularis posterior is more intimately tied to the processus paracondyloideus of the exoccipital cartilage by a ridge-like swelling of the *commissura exoccipito-capsularis*.

The anterior border (Pl. XV) commences above at the anterior end of the superior border or to be more precise perhaps, at the anterior end of the prominentia utriculo-ampullaris superior. It is hidden from view by the petro-squamous venous sinus (the intracranial part of the lateral jugular vein). It descends with a slight forward inclination and is indented by the crus breve of the incus cartilage to form a shallow *fossa incudis*. Below this the anterior or basal border rapidly projects forwards to culminate in the *crista parotica* to which is attached the cartilaginous styloid process (*tympano-hyae*); from this projection the lower half of the anterior border descends and recedes forming here the lateral wall of the *fossa musculi stapedii*, which is of very large size. The anterior border terminates below at the *prominentia utriculo-ampullaris inferior*.

The *lateral surface* is remarkable for two things, viz. the presence of a large vacuity which lies under the prominentia semicircularis anterior, and for the presence of an enormous *prominentia semicircularis labialis* (fig. 3) which runs almost vertically upwards close behind the anterior border. As it passes upwards it increases in prominence because it is here forming its ampullated anterior extremity. To the lateral surface immediately lateral to the cupola, the supraoccipito-capsular commissure is attached.

The *medial or supero-medial surface* (Pl. XVII) is ovoidal in form, longer vertically than from before backwards.

It is bounded above by the prominentia semicircularis superior, above and anteriorly by the prominentia utriculo-ampullaris superior, behind by the downward continuation of the prominentia semicircularis anterior, below by the *crus commune* of the anterior and posterior semicircular canals, below and anteriorly by the hind wall of the vestibular segment of the pars cochlearis

of the auditory capsule. These structures in the order mentioned complete the ovoidal boundary of the supero-medial surface of the pars canalicularis. Within the confines of this boundary the remainder of the supero-medial surface is sunk very deeply to form the *fossa subarcuata anterior* and at the bottom of the upper third or so of this fossa a large vacuity is met with which in the cartilaginous skull communicates with the exterior although with all the parts in position it is closed by membranous tissue and by the posterior inferior angle of the parietal bone. As will be seen from the accompanying drawing (fig. 1) this large fossa lodges the paraflocculus. The *infero-mesial* surface (fig. 1) is partly visible from the cavum cranii and partly so from the exterior. The two parts are separated from one another by the exoccipito-capsular commissure. The caval part of this surface forms the roof of what corresponds with the *recessus supra-alaris* in other animals, which lodges in the main the lower end of the lateral venous sinus, together with the exit parts of the ninth, tenth and eleventh cranial nerves. The extracaval part of the infero-mesial surface is somewhat concave, placed between the posterior semicircular canal above and externally and the exoccipito-capsular commissure medially (fig. 1). It is depressed between these structures to form a fossa subarcuata posterior, which is limited anteriorly by the *prominentia utriculo-ampullaris inferior* (not shown in plates).

The *basal* surface of the pars canalicularis is partly confluent with the vestibular segment of the pars cochlearis, i.e. in its medial half, whilst the lateral half or so is free, forming the cartilaginous posterior wall of the primary tympanum. It is bounded medially by the vestibular segment of the pars cochlearis, laterally by the boundary common to it and the anterior border of the lateral surface of the pars canalicularis. This common border has been described in connection with the lateral surface in question so it need not be further alluded to. From the uppermost part of the free part of the basal surface the tegmen tympani projects forwards and downwards with a curious sinuous course. It finally bends inwards towards the "cochlear" segment of the pars cochlearis and ends in a pointed extremity (Pl. XIII). The tegmen tympani is covered above, though a fairly considerable interval separates them, by the backward extension of the alisphenoid (Pls. XIII, XVII). More posteriorly the relation between the two becomes more intimate. On the medial side of its root commences above the tympanic segment of the sulcus facialis. When this sulcus is traced downwards it is found to become confluent with the sulcus which lodges the stapedius muscle and which is of enormous size (Pl. XIV).

The pars cochlearis (Pls. XIII, XIV, XVII) may be divided, following Voit—as I have done in respect to this region in other communications—into a "vestibular" and a "cochlear" segment(3). It is of large size, and contains the membranous cochlear duct, the saccule, the utricle and the ampullae of the semicircular canals.

The whole pars cochlearis is directed towards the central stem and viewed from the front seems to run almost at right angles inwards from the pars

canalicularis. The apex of this region is directed forwards. To the pars cochlearis just above the apex or cupola of the cochlear segment of the pars cochlearis the anterior trabeculo-cochlear commissure is attached. The greater part of the pars cochlearis is seen in the adult animal with very much the same appearance as in the foetal state—there being practically no superadded bone.

We may now consider the segments of the pars cochlearis which it will be remembered are the vestibular and the cochlear.

The *vestibular* segment presents for examination a medial or caval, an inferior superior and an infero-lateral surface.

The *medial* or caval surface (Pl. XVII) is identified by the fact that it is perforated by two openings, one the foramen acusticum superius + foramen faciale, the other the foramen acusticum inferius. These two openings are separated from one another by a broad bar of cartilage which is the crista falciformis. The upper opening is single, that is, the facial canal and the foramen acusticum superius are confluent but the facial and superior vestibular nerves occupy the usual relative positions, that is, the facial nerve is the more medial.

The lower foramen or foramen acusticum inferius transmits the cochlear nerve and the inferior division of the vestibular. From the inferior division of the vestibular nerve a large branch is directed through a special foramen to the lower part of the saccule and the lower wall of this foramen is ossified. There is likewise a *foramen singulare* in the hinder wall of the foramen acusticum inferius to transmit the nerve to the ampulla of the posterior semicircular canal. There are no separate foramina in either cartilage or bone for the branches of the cochlear nerve at this stage. Both the foramen acusticum superius + facial canal, and the foramen acusticum inferius are sunk at the bottom of a very slight depression which is the meatus auditorius internus.

Above the foramen acusticum superius + foramen faciale is a prominent *commissura suprafacialis* which is prolonged backwards and outwards to form a prominent crest (Pl. XVII). This afterwards becomes ossified and retains in that form practically the same form as in the cartilaginous condition. The whole bony auditory capsule which can readily be disarticulated resembles very closely the cartilaginous one and the semicircular canals appear much as in the usual carefully prepared article of commerce.

The *inferior* surface is convex from side to side and may be said to stretch inwards from the foramen rotundum (cochleae) to the medial margin of the foramen perilymphaticum which is thus to be regarded as forming a perforation in the inferior wall of the vestibular segment of the pars cochlearis. The foramen itself lies just above the foramen jugulare and cannot be seen in the plates.

The *infero-lateral* surface forms part of the medial wall of the tympanic cavity (fig. 5). It shows from above downwards the sulcus facialis, which lies somewhat medial to and below the tegmen tympani; the foramen ovale (vestibuli), which is occupied by the foot of the stapes cartilage and below the foramen ovale, the foramen rotundum which is in the usual position.

The "cochlear" segment is of comparatively large size and exhibits on its anterior aspect the number of its coils as a well-marked sulcus septi spiralis is present. This appearance is fully maintained in the fully ossified condition. The apical region is placed forwards and there is attached to it the anterior chordo-cochlear commissure which at this stage appears to go backwards from the ala temporalis.

(*c*) *The Ala temporalis* (Pls. XIII, XIV, XVII).

Only a small part of this cartilage remains unossified and it would be difficult to hazard a guess as to what its limits and extent are at an early stage. So far as can be seen it is in direct continuity posteriorly with the anterior chordo-cochlear commissure whilst mesially and posteriorly it is in direct contact with the ossified processus alaris of the pars trabecularis which is here ossified to form the os post-sphenoidale although there seems to be signs of an original separation between the two. At about the middle of its lateral edge the cartilaginous ala temporalis is notched by the mandibular division of the fifth cranial nerve. Good views of it are obtained by inspection of Plates XIII and XIV. In Plate XIII, the investing covering of bone has been removed from the upper side, where it is seen to be bounded medially by the post-sphenoidal centre with perhaps processus alaris likewise bony, in front of which is the upper lamina of the pterygoid bone. Laterally and in front is seen the alisphenoid and at the expense of the latter chiefly the foramen ovale is seen bounded medially by cartilage. On the right side in Plate XIII all bone has been removed save that which may be processus alaris (if this ossify independently). It is to be noted that the anterior trabeculo-cochlear commissure is unossified at this stage.

(*d*) *The Ala orbitalis* (Pls. XIII, XIV, XV, XVI).

This resembles in many respects that of *Microtus amphibius* and chiefly because the post-optic limb of the ala fails to meet the upper aspect of the root of the *ala hypochiasmata* and so close in the foramen opticum. This foramen then is absent, is represented by a notch in the hinder border of the ala orbitalis which may be called the *incisura optica* (Pl. XIII), and the optic nerve passes through this notch to the orbit. This condition may be regarded as transitional between that of the marsupial in which the incisura is not even present (Dasyurus) and the higher mammals in which a complete foramen opticum is the rule. The main mass of the ala orbitalis is somewhat triangular in form having the apex directed towards the central stem with whose inter-orbito-nasal segment it is fused. This apical part represents only the pre-optic limb of the ala orbitalis. The base has projected forwards from its anterior basal angle its share of the *spheno-ethmoidal commissure*, which anteriorly having bounded on its lateral aspect the *orbito-nasal fissure* fuses with the backwardly directed process from the prominentia frontalis of the pars intermedia of the lateral nasal capsule. The posterior basal angle is continued

backwards into the *orbito-parietal commissure*. Both of these commissures are slender. The anterior border of the ala temporalis is sharp and forms the hinder boundary of the orbito-nasal fissure; the posterior border of the ala forms the anterior or superior border of the sphenoidal fissure which is here bounded posteriorly by the ossified alisphenoid.

The ocular muscles are the usual recti with a retractor bulbi and two obliques. All save the obliques take origin from the ala hypochiasmata. The superior oblique arises from the ala orbitalis behind the orbito-nasal fissure and some considerable distance from the incisura optica. The inferior oblique arises from the maxillary prominence of the pars intermedia of the nasal capsule immediately below the os lacrimale (Pl. XIV).

(*e*) *The Lateral Nasal Capsule.*

This at this stage is very completely chondrified, and is exceedingly complicated; moreover it is of considerable length, but its detailed description will be reserved until later.

3. Lateral Structures (Pls. XIII, XIV, XV).

These paired structures are:

(1) The supraoccipital cartilage.
(2) The lamina parietalis (parietal plate).
(3) The ala orbitalis.

(1) *The supraoccipital cartilages* are to a very large extent ossified, only the more anterior part remaining entirely cartilaginous, and fusion with the exoccipital cartilage below is so complete that it is not possible to define its lower extent with any certainty. From what remains of it however it would seem to have been of triangular form, with base forwards, and the upper basal angle is directly continuous by what I have elsewhere—Poecilophoca, p. 426—named a *commissura supraoccipito parietalis*, a slender commissure which forms the upper boundary of the *supraoccipito-capsular fissure*. The inferior basal angle is in part fused with the auditory capsule just lateral to the point where the posterior limb of the anterior semicircular canal blends with the corresponding limb of the posterior semicircular canal to form the crus commune, forming here a *supraoccipito-capsular commissure*. The apical region of the supraoccipital cartilage is entirely ossified so that one cannot say what its earlier form was.

(2) *The laminae parietales*. Each lamina parietalis is of triangular form, attached by its apex to the anterior end of the corresponding anterior semicircular canal. This apex separates the *supraoccipito-capsular fissure* behind from the large *spheno-parietal fontanelle* in front. It is covered by the parietal bone which is separated from immediate contact with the apex by the vena capitis lateralis (Pl. XV) on its way from the cavum cranii to the post-glenoid foramen. The posterior basal angle is fused with the anterior basal angle of

the supraoccipital cartilage to form the supraoccipito-parietal commissure. The anterior basal angle fuses with the posterior basal angle of the ala orbitalis to form the long and slender orbito-parietal commissure. Practically the whole of the lateral surface of the lamina parietalis is covered laterally by the parietal bone (Pls. XV, XVI).

(3) The *alae orbitales* have already been described.

The Lateral Commissures (Pls. XV, XIII)

These from behind forwards are:

(*a*) The supraoccipito-parietal.

(*b*) The orbito-parietal.

(*c*) The spheno-ethmoidal.

The separate treatment of these structures is convenient because they help to form the rim or brim of the cavum cranii. Each is narrow and slender and the names given to each are topographical. Their precise limits and mode of formation cannot be given on account of the complete state of chondrification here presented. The following points are of interest in regard to them. The orbito-parietal commissures are entirely covered laterally by the parietal bone of their side, and the spheno-ethmoidal commissure is embraced on both its inner and outer sides by the frontal bone, because the orbital plate of that bone has begun to spread in as a covering bone towards the cribriform plate of the cartilaginous ethmoid (Pl. XIII). The part of the frontal bone which immediately covers the caval aspect of the spheno-ethmoidal commissure is very narrow, but the bone widens out having crossed the commissure and almost completely blocks up the orbito-nasal fissure, only a small canal being left for transmission of the nasal nerve from the orbit to the region of the cribriform plate. This canal is naturally the anterior ethmoidal canal. The course of the nasal nerve was first explained by the late Prof. Gaupp, and I think this is a stage which would have greatly interested him. The spheno-ethmoidal commissure is connected anteriorly with the frontal prominence of the pars intermedia of the nasal capsule as it always is.

As has been said, these commissures take part in the formation of the cranial rim or brim, which is formed on each side from behind forwards by the supraoccipital cartilage (here largely ossified), the supraoccipito-capsular commissure, the basal edge of the lamina parietalis, the orbito-parietal commissure, the spheno-ethmoidal commissure and the anterior curved border of the caval aspect of the lateral nasal capsule; to these may be added in the anterior median line, the prominent and backwardly curved crista galli.

4. Dorsal Commissures (Pls. XIII, XIV).

The only commissure which can be alluded to under this title is the tectum cranii posterius, but as it is here ossified to form the supraoccipital bone nothing more can be said about it.

The Nasal Capsule (Pls. XIII, XIV, XV, XVI, XVIII, XIX).

This structure is of extraordinary interest and complexity especially anteriorly. It consists of a septum and two lateral appendages which are conveniently named the lateral nasal capsules. It is of large size and its total length is equal to that of the central stem behind it. In general shape as viewed from above (Pl. XIII), it is pyriform, the large end being posterior, and its greatest width is at the site of attachment of the inferior oblique muscles of the eyeball (Pl. XIV). As it is traced forwards it becomes laterally constricted at about the junction of the anterior fourth with the remainder; beyond, i.e. anterior to, this constriction, the capsule expands somewhat and in this region a well-marked median sagittal sulcus dorsalis nasi becomes evident separating the two cupulae anteriores from one another.

The capsule as a whole may be regarded as presenting for examination from the exterior three surfaces, viz. a superior or dorsal, an inferior and a lateral surface.

The *superior or dorsal surface* (Pl. XIII) is large and as part of it is directed towards and forms part of the floor of the cavum cranii (the remainder being extra-caval), it may be divided into a caval or subcerebral and an extra-caval or precerebral part.

The caval surface will be described first.

The caval surface is of large size, ovoidal—very nearly circular—in form, and slightly compressed from above downwards so that its transverse is greater than its antero-posterior diameter. This part of the dorsal surface is so inclined as to be very nearly vertical, hence nearly at right angles to the extra-caval part. It is divisible into two symmetrical halves by a line drawn sagittally through the dorsal aspect of the septum nasi, which septum becomes evident along the anterior half of the median sagittal line drawn through this segment of the dorsal surface, and it rises cavally to end above in a large pointed and somewhat recurved *crista galli* (Pl. XV) which is covered by the meeting of the two frontal bones at the metopic suture.

Each half of the caval (subcerebral) surface is divisible into an anterior and a posterior part; of these two the posterior is flat and complete and passes without break of continuity medially into the dorsal part of the septum nasi. For this part I suggest the name *pars imperforata*. It is continuous laterally through the orbito-nasal fissure with the planum antorbitale of the lateral nasal capsule. In front of the pars imperforata, which may be regarded as having an anterior concave margin, is the anterior segment of the caval surface. At this stage the pars imperforata is being covered by the orbital plate of the frontal bone and being therefore excluded from the cavum cranii. Over it, under the orbital plate of the frontal bone, the nasal nerve courses to reach the cavum before crossing the lamina cribrosa. This, nearly circular in form, is perforated by the roots of the olfactory nerve and may be called the pars perforata. It is identical with the lamina cribrosa (cribriform plate).

The foramina in this region are divisible into at least two main groups, viz. a postero-median and an antero-lateral group, and an antero-posterior lamina of cartilage separates them. This corresponds with the crista intercribrosa of Voit. It differs only in its direction from that in the rabbit which Voit described and in Microtus described by myself. In the two latter there is crista intercribrosa (Pl. XIII) which runs from behind obliquely forwards and inwards towards the septum nasi. Here there is a lamina in place of a crest and it is directed parallel with the sagittal plane. It may be pedantic to describe it as the *lamina intercribrosa*, though it really is more than a crest. To its medial side the medial olfactory foramina are situated, and along its posterior edge numerous posterior foramina are met with which together with the median foramina constitute the postero-median group. Immediately in front of the most anterior median foramen a large circular foramen is met with. It transmits the nasal nerve to the nasal cavity. This nerve is of enormous size and retains its circular form for some time after it has entered the nasal cavity (fig. 10).

The extra-caval or precerebral part of the dorsal surface of the nasal capsule is separated from the caval part by a sharp boundary caused by the almost rectangular inclination of the one to the other. It is wide posteriorly and divisible into two primary parts, viz. a posterior constituting about one-third of the whole, and a remaining anterior two-thirds.

The posterior third is separated from the anterior two-thirds by a somewhat deep sulcus which is the *sulcus antero-lateralis* (Pls. XIII, XV, XIX) and which is perforated at the site of junction of the dorsal with the lateral surface of the capsule by a very small foramen epiphaniale (Pl. XIX). This segment of the dorsal surface is the *prominentia frontalis* of the pars intermedia of the nasal capsule. It is overlapped by the frontal bone. It will be seen later that the prominentia frontalis is the outward expression of the recessus frontalis. Professor Terry(4) has in his careful and interesting study of the primordial cranium of the cat suggested that the foramen epiphaniale is the remnant of the fissure which separated the parieto-tectal from the paranasal cartilage of his terminology. That the nasal capsule does appear to develope in this way I believe to be true; it certainly is the case in *Bos* as the plate accompanying my communication on Erinaceus(5) shows and as Noordenbos(6) has seen, but it had not occurred to me to account for the foramen epiphaniale in the way Terry I think rightly does, and the suggestion may be extremely helpful in the understanding of this region.

The anterior two-thirds of the extra-caval or precerebral surface is divisible into approximately two halves, viz. a posterior and an anterior by means of the annular constriction previously alluded to, a constriction due possibly to the limitations imposed on peripheral expansion by the junctional regions of the frontal and premaxillary bones in this position. The hinder half of this segment is overlapped by the frontal bones to a considerable extent and they nearly meet in the middle line over it, but anteriorly they diverge from one another leaving a large angular gap between them which completely exposes

the dorsal aspect of the capsule to view (Pls. XIII, XVI). This part of the dorsal surface is slightly concave from side to side, but although separated from the lateral surface of the capsule by a rounded margin, the change from one surface to the other is unusually abrupt, giving a squareness to coronal sections of this region not commonly met with.

The anterior half of this segment of the dorsal surface, viz. that part in front of the annular constriction above mentioned is completely free and uncovered in any way by bone. I have been unable to identify a separate os nasale either in the specimen modelled or in the skull of an adult animal macerated from a specimen kindly given me by Prof. J. P. Hill. Nasalia are described by some authors as narrow splint-like bones lying medial to the frontalia, but I have been quite unable to identify them here and I scarcely think that they can have developed independently by this stage and fused with the frontalia. As this part is traced forwards it appears to bifurcate into two hemispherical projections each of which is separated from its fellow by a well-marked sulcus dorsalis nasi (Pls. XIII, XVIII). These hemispherical projections are the cupulae nasi anteriores. Each at its basal part is in close relation with the upward and backwardly directed processus alaris inferior (Pls. XIII, XV, XVIII, XIX).

We may now turn our attention to the lateral wall of the nasal capsule as seen from the exterior (Pls. XV, XIX).

The *external* aspect of the *lateral* wall of the nasal capsule shows clear signs of demarcation into the usual three parts which are from behind forwards, the *pars posterior* or pars ethmoidalis, the *pars intermedia* or fronto-maxillaris and the *pars anterior*.

These parts are separated from one another in much the same way as usual; thus, the pars posterior is separated from the pars intermedia by the *sulcus postero-lateralis*, which at the same time indicates the position of the first ethmo-turbinal in the interior. The pars intermedia is separated from the pars anterior by the *sulcus antero-lateralis*.

Of these parts the pars posterior is the smallest, the pars intermedia the deepest, and the pars anterior the longest from before backwards.

The *pars posterior* is directed downwards and backwards from the pars intermedia. It is continuous through the orbito-nasal fissure with the pars imperforata of the caval segment of the dorsal part of the nasal capsule. Laterally it is directed towards the eyeball, so this part may be spoken of as the planum antorbitale. Its hindmost part is incomplete so there is no cartilaginous cupula posterior and, as viewed from the side, a vacuity takes the place of the cupula which is bounded below by a short backwardly directed process which bears some resemblance to the processus maxillaris posterior of the reptilian nasal capsule. This process is covered by the lamina perpendicularis of the os palatinum. It will be seen later that the absence of a true cupula nasi posterior leads to absence of the lamina transversalis posterior from the solum nasi.

The *pars intermedia* is the deepest part of the lateral aspect of the nasal capsule and is isolated by the antero-lateral and postero-lateral sulci. It is divisible into at least two parts, viz. a superior and an inferior. The superior part projects as the prominentia frontalis, of which a part has already been seen from above. The inferior part is directed towards the maxilla and from it there projects a small elevation which is the processus maxillaris anterior. From the most lateral part of the prominentia maxillaris the inferior oblique muscle takes origin, immediately above which lies the small perforated os lacrimale, with the naso-lacrimal duct passing forwards through it. Towards the lower edge of the maxillary prominence of the pars intermedia a longitudinal ridge is met with which can be traced from the processus maxillaris anterior to the processus maxillaris posterior. This ridge bounds laterally a sulcus whose inner margin is free and forms the hinder part of the lower edge of the maxillo-turbinal. The sulcus in question is caused by the mucosa of the nasal passage turning outwards and upwards below the maxillo-turbinal, which is of comparatively small size.

The *pars anterior* as viewed from the lateral aspect is long from before backwards, narrow from above downwards, and narrower in front than behind. It is somewhat quadrilateral in form with the base backwards wider behind than in front. It reaches from the antero-lateral sulcus behind to the lateral margin of the anterior narial aperture in front. The upper border is rounded and through it this aspect is continuous with the dorsal aspect of the capsule. The inferior border is sharp and divisible.

We may now consider the floor of the nasal capsule or *solum nasi*.

The *solum nasi* is incomplete, but what it lacks is fully compensated for by its complexity. It may be said to consist of from before backwards, the following structures, viz. the ali-cupular commissure, the medial part of the processus alaris inferior, the lamina transversalis anterior, the anterior paraseptal cartilage, the posterior lamina of the cartilage of the naso-palatine duct, and finally the posterior paraseptal cartilage.

The *ali-cupular commissure* represents a part of the incomplete ring-like base of the cupula anterior of the capsule. It stretches from the medial wall of the anterior nasal aperture with a curved course, concave upwards to fuse with the middle of the anterior border of the processus alaris nasi inferior. It is separated from the processus lateralis ventralis of the septum nasi by a vacuity over which lies the nasal mucosa.

The medial part of the processus alaris inferior projects medially and backwards on the lateral side of the vacuity just mentioned and finally ends as a lacrimal spur on the outer side of the fissure through which the naso-lacrimal duct enters the interior of the nasal capsule, and on the outer side too, of the lamina transversalis anterior.

The *lamina transversalis anterior*. This is a very curious structure and not at all easy to describe. On the whole one may perhaps describe it best as a somewhat triangular plate whose anterior and posterior sides are free, and

whose base is directed upwards towards the lower margin of the lateral wall of the nasal under cover of the naso-lacrimal duct over which it fuses with the lower border of the said lateral wall. The length of the line of fusion is smaller than the total length of the base of the lamina so that a small incisura post-transversalis and a small incisura pre-transversalis separate the base in part from the lower margin of the lateral wall of the nasal capsule. Through this anterior incisure the naso-lacrimal duct passes into the interior of the nose, and the outer side of the incisure is covered by the lacrimal spur of the processus alaris nasi inferior. On account of the shortness of the basal attachment when compared with the total length of the basal border of the lamina I have marked this attachment on Plates XIV and XIX as the superior process of the lamina-transversalis anterior. It is the part which is also bent upwards as the atrio-turbinal. N.B. The indicating line in the plates has been carried too far forwards; it actually points to the lacrimal spur of the processus alaris nasi inferior.

The anterior basal angle of the lamina transversalis anterior is prolonged forwards as a long slender process as far as the processus lateralis ventralis, but it does not fuse with that structure. To this process I have given the name processus anterior of the lamina transversalis. It lies below the septum nasi and is separated from it by a downward projection of the nasal mucosa.

The apical part of the lamina transversalis anterior is twisted at right angles to the main mass (whose surfaces are infero-lateral, and supero-medial) so that its surfaces are fore and aft. This apical region is connected below with the anterior paraseptal cartilage medially and with the cartilage of the naso-palatine duct laterally.

The surfaces of the main mass of the lamina transversalis anterior are infero-lateral and supero-medial, but the whole direction of this part of the lamina is nearly vertical; by its supero-medial surface it is in relation with the nasal-mucosa, and by its infero-lateral surface it is in relation with that part of the os incisivum which forms the medial wall of the first incisor tooth socket. The apical region whose surfaces are twisted fore and aft, is in relation by its anterior surface with the commencement of the paraseptal process of the os incisivum which sweeps outward in front of this region (fig. 14) to later pass backwards on the medial side of the anterior paraseptal cartilage, and terminate a little distance in front of the vomer. Immediately behind the continuity of the apical region of the lamina transversalis anterior with the anterior paraseptal cartilage the duct of the organ of Jacobson turns upwards and outwards in a tunnel (fig. 9) of the latter to join the naso-palatine duct (fig. 10).

The *anterior paraseptal cartilage* (Pls. XIV, XV, XVIII, XIX, figs. 8, 9, 10, 11) is large and complex. Its large size corresponds with the large size of the organ of Jacobson which is lodged in its lateral concavity. Its description may commence for convenience at its posterior extremity which is placed at a point half-way along the infero-lateral border of the septum nasi.

The cartilage commencing in a pointed posterior extremity soon becomes of a plate line form with long axis directed almost vertically. This form it retains until the organ of Jacobson is reached where this plate becomes curved with its concavity outwards and the organ is lodged in the concavity, and as a consequence the plate may be regarded as consisting of a medial and an infero-lateral wing. This condition (fig. 8) is maintained for the greater part of the extent of the cartilage in a forward direction. On nearing the lamina transversalis the medial and infero-lateral wings of the plate fold together around the commencement of the duct of the organ of Jacobson so that it comes to lie in a tunnel (fig. 9), from which it soon emerges in an upward and outward direction in order to join the naso-palatine duct (fig. 10). The anterior paraseptal cartilage now by means of its medial limb becomes fused with the apical region of the lamina transversalis anterior (fig. 11) and from this region runs forwards in confluence with the anterior process of the cartilage of the naso-palatine duct, forming with the latter a curved hood-like cartilage which is continued as far forwards as the processus lateralis ventralis. This curved cartilage lies over the anterior part of the naso-palatine duct (figs. 10, 11). In front of the junction between the medial lamella of the anterior paraseptal cartilage with the apical region of the lamina transversalis anterior, the root of the paraseptal process of the os incisivum turns inwards to run backwards along the medial side of the medial lamella of the anterior paraseptal cartilage (figs. 8, 9, 10, 11).

The cartilage of the naso-palatine duct is of large size and great complexity. It may be regarded as consisting of a central part, attached at its upper aspect to the more lateral part of the apical region of the lamina transversalis anterior, and of two processes, one anterior, the other posterior. The central part overhangs the site of junction of the organ of Jacobson with the naso-palatine duct. The posterior process passes backwards from this region in the form of a rapidly broadening lamella which at first is placed almost horizontally under the infero-lateral lamella of the anterior paraseptal cartilage from which it is separated by the naso-palatine duct (fig. 10). At about the middle of its course it attains its maximum width, still supporting what may be termed the aditus of the naso-palatine duct, then it begins to narrow and it ends posteriorly opposite the level of the middle of the anterior paraseptal cartilage, here supporting that part of the nasal mucosa which projects down below the lower margin of the lateral wall of the nasal capsule (fig. 8).

The anterior process commences at the central part, in direct continuity with the posterior process (Pl. XVIII); it is fused at first with the medial limb of the anterior paraseptal cartilage, the two forming the curved hood-like cartilage which overhangs the forward continuation of the naso-palatine duct (fig. 11). After that duct becomes confluent with the epithelium of the mouth, this anterior process is continued forwards as a somewhat slender rod of cartilage oval in section with long axis transverse to a point below the processus lateralis ventralis of the septum nasi (fig. 15). Between the anterior processes of the

two sides a dumb-bell shaped cartilage, the cartilage of the papilla palatina, is placed (fig. 12).

The *posterior paraseptal cartilage* is the forward prolongation of the infero-medial wall of the post part of the nasal capsule. The lamina transversalis posterior whose inner basal angle generally gives origin to the posterior paraseptal cartilage being in this instance absent. It is of considerable length and passes forwards alongside the infero-lateral border of the septum nasi separated from it by the corresponding lamella of the vomer (Pl. XIV).

The *interior* of the nasal capsule may now be considered.

The *septal* wall is low posteriorly but rapidly increases in depth, entirely by increase towards its upper end, the lower edge remaining constant. The highest part of the septal wall is that which culminates as the crista galli which, as already pointed out, is of large size, pointed at its extremity which is somewhat curved backwards. All the part of the septal wall posterior to the spring of the crista galli is subcerebral (subcaval); the remainder gradually falls in height at the expense of the upper part. At the anterior end this wall is everted partly as the processus lateralis ventralis, partly as the medial part of the cupola nasi anterius. There is no internarial foramen in the septum.

The *lateral* wall of the nasal cavity shows the three usual parts, viz. the pars anterior, pars intermedia and the pars posterior.

The first is separated from the second by a somewhat faintly expressed crista semicircularis, the second from the last by the root of attachment of the first primary ethmo-turbinal.

There is little to be said concerning the internal surface of the pars anterior. No sign of a cartilaginous naso-turbinal is visible although a swelling of the mucous membrane hints at the possibility of there being such at a later date.

The pars intermedia is divisible into an upper and lower recess, both of which are continuous over the lower end of the crista semicircularis. The upper recess is the recessus frontalis, the lower is the recessus maxillaris. The upper or frontal recess receives several branches of the olfactory nerve through foramina in the antero-lateral part of the lamina cribrosa which forms its roof. It is to a large extent shut off from the recessus maxillaris by the first ethmo-turbinal which forms a considerable part of its floor.

The *recessus maxillaris* is of large antero-posterior extent and contains in its antero-lateral part the lateral nasal gland so that it almost might be termed the recessus maxillo-glandularis. It is confluent above and in front of the first ethmo-turbinal with the recessus frontalis. Anteriorly it is continued into the cavity of the pars anterior, whilst it is overhung to a large extent by the first primary ethmo-turbinal. It opens out behind directly into the ductus naso-pharyngeus as the apex of the cupular region is awanting.

The *pars posterior* is small, deficient below and behind. It persists dorsally as the lamina imperforata and medially as the posterior paraseptal cartilage. It receives numerous branches of the olfactory nerve through the post group of postero-median foramina which descend along the nasal surface of the

lamina imperforata. It is limited antero-laterally by the first primary ethmo-turbinal which separates it from the pars intermedia. Its interior is complicated by two turbinals which project sagittally from the lamina imperforata. These are the second and third primary ethmo-turbinals and the third is about half the size of the second. The second is less than half the size of the first.

The *anterior narial aperture* may now be considered.

The aperture consists of an anterior and a lateral part. As a consequence the cupula anterior is deficient anteriorly and laterally, and is represented only by an incomplete ring-like base open outwards. The component parts of this incomplete ring are, above and supero-laterally, the *tectum nasi* and the lateral wall, terminating in a *processus alaris nasi superior*, respectively. Medially is the corresponding lamella of bifurcation of the septum, inferiorly the *ali-cupular commissure*, and infero-laterally the *processus alaris nasi inferior*. The lateral segment of the anterior narial aperture is directed outwards and upwards along the processus alaris nasi inferior, and bounded above by the processus alaris nasi superior. Posteriorly at its commencement it is bounded by the anterior border of the lateral wall of the nasal capsule which is bent inwards by the outgoing mucous membrane and the maximal inbending may be spoken of as a *margino-turbinale* since it supports from below a considerable mucous turbinal which projects into the interior of the nose (Pl. XVIII and fig. 15). This turbinal is in line with the atrio-turbinal caused by the inflexion of the superior process of the lamina transversalis anterior and that in turn is in line with the maxillo-turbinal. The mode of formation of this region is best understood after reading the account of the nasal capsule of *Tatusia novemcincta* which follows this communication.

The *processus alaris nasi inferius* is of very large size. It springs from the lower part of the anterior border of the lateral wall of the nasal capsule and runs at first outwards with upper concave surface and lower convex aspect. It then twists somewhat on itself so that its upper surface becomes first medial then anterior, its lower surface thus being first lateral then posterior; finally contouring the lateral aspect of the nasal capsule it ends freely in a sharp point. It sends backwards from its root a small angular spur which projects over the naso-lacrimal duct where that is entering the naso-lacrimal fissure, and below this overlaps the outer surface of the lamina transversalis anterior just above and behind the root of the processus anterior of that cartilage (Pl. XVIII, fig. 13). The processus alaris nasi inferior is joined not far from the middle of its anterior border by the ali-cupular commissure (Pl. XVIII), which ties it to the septum nasi through the intermediation of the medial part of the ring-line base of the cupula nasi anterius.

Before leaving the subject of the nasal capsule one may allude, and with pleasure, to the work of Terry on the subject in his communication on the primordial cranium of the cat. Working with van Wighe's methylene blue method he has been able to show at the 18–20 mm. stage that the lateral wall

of the nasal capsule is laid down in three segments, which correspond very closely with the three segments already described here. These segments he describes as parieto-tectal which corresponds with the pars anterior, a part which may or may not be an outgrowth of the septum, another segment which he calls the paranasal cartilage developed independently is separated in front by a fissure which becomes the foramen epiphaniale when for the most part closed. The paranasal cartilage always gives attachment to the max. obliquus inferior oculi and corresponds with the pars intermedia; the hindmost segment, which he calls the lamina antorbitalis, corresponds with the pars posterior. The mutually inrolled approximated edges of the two anterior segments produce the crista semicircularis thus: the crista semicircularis is formed by the anterior edge of the paries nasi and the posterior edge of the pars parieto-tectalis. There is I think every reason to believe that Terry is right, and his observation and interpretation of the facts are most helpful in the solution of a previously very difficult point.

We may now pass to the consideration of the visceral cartilages.

The Cartilages of the Visceral Arches (Pls. XV, XVI).

The cartilaginous skeleton of the first visceral or mandibular arch are three in number, viz. from behind forwards: the incus cartilage, the malleus cartilage and Meckel's cartilage.

The incus cartilage gives one the impression of being somewhat small. It shows the usual parts and so far as I can see has the usual relations. Its crus breve rests in a small fossa incudis placed some distance above the upper end of the root of the crista parotica. The whole cartilage is overhung by the vena capitis lateralis on its forward course to the post-glenoid region. The crus longum articulates with the head of the stapes cartilage in the usual way.

The *malleus* cartilage strikes one as being very large, the head and neck especially so. A well-marked crista mallei descends as a curved ridge concave backwards just in front of the incus malleus joint. The manubrium is short and directed inwards almost at right angles to the rest of the cartilage. Ossification has commenced in the head of the cartilage.

From the front of the head the next cartilage projects forwards. Meckel's cartilage is long, comparatively slender, and cylindrical. It passes forwards and gently downwards, gradually converging on its fellow. A short distance behind the mental foramen it sinks into the mandible to again emerge not far from the anterior end of the bone after which it unites with its fellow. Just in front of the head of the malleus cartilage a long goniale covers the under aspect of Meckel's cartilage.

The cartilages derived from the second visceral arch are the stapes and the processus styloideus or Reichert's cartilage. The stapes cartilage is much of the usual type but has an enormous stapedius muscle inserted into it. It is perforated by a tolerably large stapedial artery which is larger than the onward continuation of the internal carotid artery from which it is derived.

Reichert's cartilage is of considerable length. It starts as the direct continuation of the apex of the crista parotica and descends almost parallel with the neck of the malleus cartilage. It now changes its direction, passing forwards and somewhat inwards with a marked concavity upwards; next it arches forwards and inwards, then downwards, and comes to an end in a pointed extremity just behind the junction of the corpus hyale with the thyro-hyal—for a considerable stretch in front and behind its middle the cartilage is ossified.

The cartilage of the third visceral arch, namely the thyro-hyal, is of large size, commencing behind in a somewhat inbent pointed extremity. It curves outwards for a short distance and gives off a large descending process, after which it rapidly narrows. It runs into the lateral angle of the corpus hyale without any histological line of demarcation.

The *corpus hyale* or 1st basi-branchial is of a very ordinary type and much resembles that of man in form.

In the model it lies across the front of the thyroid cartilage opposite the middle of the latter.

The cartilage of the *fourth visceral arch* is represented by the thyroid cartilage, which is of large size especially from before backwards. It consists of two alae which are at this stage completely fused in the middle line. Each ala commences behind at a preposterior border whose lower angle of junction with the superior border of the ala is prolonged downwards as a curved articular bar to articulate with the cricoid cartilage and from the lateral aspect of the junction of this inferior cornu or articular process a strong short muscular process projects. A superior cornu is developed at the usual site and is in direct cartilaginous continuity with the posterior end of the thyro-hyal. At the symphyseal region of the two alae in front no pomum Adami is developed which is the usual arrangement in the lower mammals. From the back of the upper part of the symphyseal region a small spur of cartilage projects in a backward direction.

The cartilages of the fifth visceral arch, viz. the cricoid and the arytenoids, are of large size, but do not present anything much out of the common in form. From the antero-lateral part of the ring of the cricoid two large muscular processes project directly outwards. The arytenoid cartilages are well developed and each of their recognised and usually described parts is well developed.

The whole larynx gives one the impression of being somewhat disproportionally large in comparison with the rest of the cranium.

THE OSSEOUS SKELETON (Pls. XIII, XIV, XV, XVI, XVII, XVIII, XIX).

Both ecto-chondral and ento-chondral bones are met with, and the former are in a high degree of development.

So far as can be ascertained no separate nasalia are present.

The *os frontale* is of large size extending forwards over the nasal capsule, hiding from view the frontal prominence of the pars intermedia, then extending

as a long somewhat triangular process over the posterior half or so of the pars anterior, articulating as it goes along with the maxilla and the premaxilla. The medial margin of the anterior nasal process rapidly cuts away as it is traced forwards, so that when the two frontalia are viewed together in the adult a large nasal notch appears between them, and the same would hold good in this case had the bones been modelled on both sides; through this nasal notch the cartilaginous nasal capsule projects in a forward direction. Behind the extra-caval part of the nasal capsule the frontal bone rapidly expands to form a large curved plate which articulates in a metopic suture with its fellows of the opposite side and posteriorly is overlapped by the anterior edge of the parietale. This plate when traced downwards covers on its lateral aspect the ala orbitalis and the spheno-ethmoidal commissure, but it also sends medial to the latter a narrow piece which on leaving the commissure expands to block up the orbito-nasal fissure save for a small opening the anterior ethmoidal canal through which the nasal nerve passes. This orbital plate of the os frontale then covers a considerable part of the lamina imperforata of the pars posterior of the nasal capsule. There is no sign either of a supra-orbital crest or of a post-orbital process.

The *os parietale* is of very large size and of quadrilateral outline. It forms a covering bone to the hinder part of the ala orbitalis, to the orbito-parietal commissure, the lamina parietalis, the supraoccipito-parietal commissure and lies lateral too to the anterior semicircular canal as well as the subarcuate vacuity described in connection with the auditory capsule. It also blocks up the whole of the lateral part of the sphero-parietal fontanelle below the level of the orbito-parietal commissure.

Anteriorly the parietal bone overlaps the hinder edge of the frontal, but medial to the eyeball the ala orbitalis of that position is left uncovered and to this area the superior oblique muscle of the eyeball is attached. By its anterior inferior angle the parietal articulates with the alisphenoid whilst along a considerable part of the infero-lateral splay on its inferior border it is overlapped by the squamosal. The posterior part of the inferior border has no bone to articulate with, and lies against the lateral aspect of the pars canalicularis of the auditory capsule. The posterior border overlaps and articulates with the large interparietale. The medial border forms by articulating with that of its fellow the saggittal suture.

The *interparietale* (Pl. XVI) is a large bone, and so far as can be seen is of membranous origin. It is triangular in shape, its base overlapping the supra-occipital and near the anterior basal angle it overlaps to a slight extent the supraoccipital cartilage. Its anterior border is overlapped by the posterior edge of the parietal bone. Its medial border is slightly overlapped by that of its fellow of the opposite side. In the adult skull I can see no trace of a separate interparietale.

The *incisivum* or *premaxilla* (Pl. XVI) is a quite considerable bone lodging two incisor teeth which are lodged in well-formed tooth sockets. From the

tooth-bearing mass it sends upwards and backwards into the angle between the nasal process of the frontal bone and the nasal or frontal process of the maxilla a frontal process of acute angular form which fills up the gap between frontale and maxilla. The body or tooth-bearing segment of the bone lies mainly between the annular constriction of the nasal capsule and the cartilage of the naso-palatine duct. From the medial side of this mass there passes inwards in front of the stalk connecting the lamina transversalis anterior with the anterior paraseptal cartilage and the cartilage of the naso-palatine duct a paraseptal process (Pls. XIV, XVIII, fig. 10) which bends backwards on the medial side of the anterior paraseptal cartilage in the usual way. There is no sign of any separation between this process and the rest of the incisivum such as Broom describes in the adult. I have no means of knowing whether this paraseptal process ossifies independently. It terminates posteriorly in just front of the anterior extremity of the vomer. A true palatine process of the premaxilla is absent at this stage, evidently because of the large size of the anterior paraseptal cartilage and of the cartilage of the naso-palatine duct which both project through an enormous gap between the premaxilla and the palatine process of the maxilla. This deficiency of a palatine process seems to hold good in the adult.

The *maxilla* (Pl. XVI) is of large size and consists of the usual parts. At this stage of development it consists of a body perforated by a comparatively large infraorbital canal for the transmission of a large infraorbital nerve; from this border there projects up over the hinder part of the lateral wall of the pars anterior of the nasal capsule a large plate-like frontal process which articulates in front with the incisivum, above with the nasal process of the frontal bone, but behind is for the most part free, an angular gap separating it from the orbital part of the frontal bone, a gap which is occupied by the maxillary prominence of the pars intermedia of the nasal capsule. At the lower part of the posterior margin of this nasal process of the maxilla the os lacrimale is found and is of annular form.

From the lower part as well as the posterior part of the body there projects downwards and backwards an external alveolar process which with the inner alveolar process derived from the palatine process completes the sockets for the canine, first and second premolar teeth. These sockets are at this stage complete, and the septa between them appear to be mainly formed at the expense of the outer alveolar wall. The outer alveolar wall behind the second premolar socket is formed by the zygomatic (malar) process of the maxilla, which projects backwards as a huge pointed process below the eyeball to come into articulation vertically below the hinder margin of that structure with the comparatively small slender zygomaticum (malar), which overlaps the apex of the pointed posterior end of the zygomatic process of the maxilla. This zygomatic process forms the outer alveolar wall of the sockets-to-be of the three molar teeth. There is at this time no roof to these sockets nor is there any inner wall more than the outer margin of the palatine process of the maxilla.

The tooth-sockets of the aforesaid teeth are therefore in open communication with the orbital cavity in the model. The palatine process is a large plate-like structure projected inwards from the body of the maxilla, i.e. from that part bearing more especially at this stage the sockets for the canine and premolar teeth. It is nearly square in form, with a slightly concave anterior margin which bounds posteriorly the large gap between it and the incisivum which transmits the cartilage of the naso-palatine duct and a considerable part of the anterior paraseptal cartilage. Its medial border anteriorly comes into contact with the vomer which it to a slight extent underlaps; more posteriorly this border recedes from the vomer somewhat so that a small fissure intervenes between the two. The posterior border articulates with the palatine process of the palatine bone in its whole length and from the junction of the outer end of the posterior border with the lateral border of the palatine process of the maxilla a long internal alveolar process is projected backwards on the inner side of the molar tooth-buds which is entirely independent at this stage of the outer alveolar wall above described.

The *os palatinum* is of considerable size and consists of a vertical and a horizontal or palatine plate.

The vertical plate is longer from before backwards than in height. It lies lateral to the pars posterior of the nasal capsule and forms a considerable part of the bony infero-internal wall of the orbital cavity. Its junction with the palatine process is overlapped to a considerable extent laterally by the internal alveolar process of the maxilla.

The horizontal or palatine plate is of large size, quadrilateral in form, with its postero-median and postero-lateral angles projected backwards as spurs. A large vacuity is found in the centre of the palatine plate which is of interest, because at this stage is represented a not unusual feature in the adult insectivore, e.g. hedgehog, in which vacuities are found in the adult palate bone. In the adult Miniopterus no such vacuity is met with. The postero-lateral angle of the palatine process at its junction with the vertical plate forms a tuberosity or spur which articulates with the pterygoid bone which lies behind it.

The *vomer*. This bone is of great length. It commences in front in a single median pointed extremity which lies in the gap between the hinder halves of the anterior paraseptal cartilages and it lies below the septum nasi. It rapidly increases in size below the septum, especially in breadth, but its upper surface is folded around the lower edge of the septum. When traced further back, it comes to lie medial to the two posterior paraseptal cartilages with which it is in contact and to which it acts as a covering bone. Shortly after coming into relation with the posterior paraseptal cartilages the vomer splits into two limbs each of which diverges from its fellow and goes backwards, following the outward curve of the posterior paraseptal cartilages to their respective cupulae; finally each limb comes to lie under the root of the ala hypochiasmata and is prolonged as a slender process along the side of the pars interorbito-nasalis of the central stem for a short distance.

The history of the mammalian vomer is of great interest and seems to be elucidated by tracing it from the condition seen in the marsupial Dasyurus. In that animal a figure of whose chondro-cranium appears in Broom's paper, at the 7 mm. stage no vomer is present, nor is it present in a specimen which I have modelled of corresponding age (Fig. A). In this animal there is a long pointed anterior paraseptal cartilage which stretches backwards along the infero-lateral margin of the septum nasi from the lamina transversalis anterior to the posterior wall of the nasal capsule which is in direct fusion with the septum nasi at this stage, but the anterior paraseptal cartilage stops just short of the posterior wall of the capsule.

At the 9·5 mm. stage (total length) (Fig. B) the anterior paraseptal cartilage has just reached the septal end of the posterior wall of the nasal capsule and to the medial side of its posterior end a small vomer is now present. This vomer is in two symmetrical halves, each of which is on the medial side of the corresponding anterior paraseptal cartilage. It is also projected backwards under the septum nasi for a short distance. No lamina transversalis posterior is present at this stage beyond a slight ridge on the posterior wall of the nasal capsule, but at the 25 mm. stage (Fig. C) the nasal mucosa has burrowed backwards into the thick posterior wall of the nasal capsule and caused it to protrude backwards in the form of a hollow pyramidal cartilaginous structure free of the septum and whose floor is now the lamina transversalis posterior which is triangular in shape with base forwards, and whose inner basal angle, having fused with the posterior end of the anterior paraseptal cartilage, is drawn out by what appears to be interstitial growth of this part of the septum nasi into a long slender posterior paraseptal cartilage, which is entirely free of the septum. The vomer shares in this attenuation if we may so call it so that it still stretches from the medial side of the posterior end of the anterior paraseptal cartilage past the posterior paraseptal element of the now common paraseptal cartilage and the now formed lamina transversalis anterior as far as the interorbital part of the pars interorbito-nasalis of the central stem. It is interesting to note that when the common paraseptal cartilage fails, as it tends to do in many animals, the failure is at this junctional region between posterior and anterior paraseptal cartilages, and this too is a part which tends to be surrounded by bone derived from the lateral lamella of the vomer which not only envelopes the paraseptal cartilage but invades it and causes its absorption. In all animals in which the paraseptal cartilages are laid down either as separate structures throughout fetal life or as a common paraseptal cartilage by ultimate fusion the vomer commences to ossify in relation with the medial side of the post extremities of the anterior paraseptal cartilages and it would seem that the formation of a cupula nasi posterior in the manner described, that is by a thrusting back of the posterior nasal wall in the marsupial, through the expansion of the nasal mucous sac (which would seem to be the primitive method), or by separate chondrification as in the cat (Terry), or Bos (Fawcett and Noordenbos) which is presumably

the later condition, and which leads to the formation of a posterior paraseptal cartilage, provides a scaffold upon which the vomer can extend in a backward direction, and it may explain why the vomer is usually primitively a paired bone which may be regarded then primarily as a covering bone to the medial edge of the anterior paraseptal cartilage of its side, and which extends backwards along the junctional region to the posterior paraseptal cartilage and the lamina transversalis posterior as they develope. Up to this point matters seem fairly simple: the difficulty arises when one enquires why the originally paired vomer should unite to form a single bone at the lower part of the nasal septum, and giving the generally, I think, held impression that the vomer is a covering bone to the septum nasi. Perhaps the question had better be approached by asking another, viz. why should they not fuse? They are bones placed by the side of the middle line; the paraseptal processes of the premaxillae not infrequently fuse, because it is said that the inswinging of the parts of the anterior paraseptal cartilage in relation with them which certainly in many instances occurs and in those animals more particularly in which the paraseptal processes are known to unite, e.g. cat, the nasalia likewise not infrequently fuse in the middle line, so do the frontalia normally, the parietalia tend to do so as age advances, the interparietalia and the supraoccipitalia do the same, so do the pre- and post-sphenoidalia, and possibly the single basi-occipital may have even arisen at some stage in the same way. Should then there be an inherent tendency for paramedian bones to fuse then one may perhaps infer that the vomer shares this tendency: but considering the question from another point of view and that extraneous pressure, such as has been cited as a possible cause of fusion of the paraseptal processes of the incisivum, may not the extraneous pressure of the approximating palatine processes of the maxillae have an influence in bringing together the two halves of the vomer?

These speculations merely apply to the condition in the mammal and the phylogenetic story here is purely concerned with the mammal, but it would appear as the outcome of them that the vomer may be regarded as a covering bone primarily to the paraseptal floor of the nasal capsule, and that when the necessity for such a support has gone by the development of palatine processes to the maxillae and palatines has provided a new support to the floor of the nose the vomer has transferred its allegiance to the septum nasi and appeared as a covering bone to that structure: and as such it has become U-shaped by fusion of its originally separate alae. As to its earlier phylogeny much turns on what the vomer as we know it in the mammal really is. If it be homologous with the amphibian vomer, then as is well known the two halves are comparatively widely separated from one another and the maxillae do not meet in the mid-ventral line of the skull, but if the vomer be something else, part for example of the parasphenoid, then there are difficulties. Its apparently constant relation to the anterior paraseptal cartilages and their origin from the lamina transversalis anterior together with the mode of formation of the posterior paraseptal cartilages and the connected laminae transversales pos-

terior together with the intrinsic growth of the nasal septum which stretches out the interval between the laminae transversales anterior and posterior point to the vomer as a structure which has grown backwards rather than forwards, as would appear to be necessary should it be parasphenoidal in origin. It is interesting to note that where the vomer actually encircles the junctional region of the paraseptal cartilage that that appears to be the region most likely to fail to develope as a cartilage, and that the gap is bridged over by what would seem to be the perichondrial representative of this structure prolonged from anterior to posterior paraseptal cartilages, in which a large part of the vomer developes. I have already pointed out the peculiar mode of origin of the vomer in man, in whom the anterior end has added to it a lateral independent lamella which actually invades the hinder end of the anterior paraseptal cartilage(7).

The *pterygoid*. This bone consists of the usual parts, namely an upper lamellar membranous portion and a lower cartilaginous hamulus. The former is inclined over towards the pars trabecularis of the central stem, comes into contact behind with the so-called processus alaris (anterior trabeculo-cochlear commissure), which is here partially ossified, but though coming into contact with this bone lies at a somewhat lower plane than its anterior edge, and its outer edge is overlapped by the cartilaginous forward prolongation of the temporalis as well as by the inner edge of the alisphenoid. It certainly forms a quite considerable element in the bony floor of the cavum cranii.

The hamulus is partly cartilaginous and partly bony; it is in direct antero-posterior line with the tuberosity of the palate bone and has the usual relations with the tendon of the tensor tympani muscle. The mandibular division of the fifth nerve leaves the foramen ovale lateral to the root of the hamulus.

The *alisphenoid* is a large fan-shaped bone which closes below a large part of the spheno-parietal foramen. Its base is of great length and articulates by its whole length with the medial lamella of the lower edge of the parietale. The posterior basal angle passes backwards towards the auditory capsule almost coming into contact with the facial nerve, after it has emerged from under cover of the supra-facial commissure. This angle overlies the forwardly projected tegmen tympani. The anterior basal angle reaches the hinder border of the ala orbitalis. The apical region is directed medialwards and is perforated by the foramen ovale at its middle interval to which the bone envelopes the cartilaginous ala temporalis, i.e. that part which remains unossified. Medial to this the apical region comes into overlapping contact with the lamina of the pterygoid bone and more posteriorly with the processus alaris (ossified) of the post-sphenoid. By its anterior margin the alisphenoid bounds posteriorly the sphenoidal fissure which is here confluent with the incomplete optic foramen (incisura optica). The hinder margin of the alisphenoid forms the anterior boundary of a long fissure in front of the auditory capsule (cochlear part), which is bounded medially by the anterior trabeculo-

cochlear commissure and transmits the great superficial petrosal nerve. No lamina pterygoidea externa is present.

The *squamosum*. This bone is much elongated from before backwards, and low in height. It articulates by the whole length of its upper border with the lower edge of the parietal bone much in the same way as in man. From near the front of the lower margin of the squama a slender zygomatic process passes outwards, then bends suddenly forwards lateral to the processus coronoideus of the mandible. This process then lays itself on the posterior half of the upper border of the zygomaticum with which it articulates. The under aspect of the outwardly directed part of the processus zygomaticus forms a prominent *eminentia articularis* in which is a laterally elongated mass of cartilage (fig. 18); behind this eminence is the glenoid fossa whose long axis is transverse. It articulates with the processus condyloideus (which is likewise transversely elongated) of the mandible. Behind the glenoid cavity is a very prominent post-glenoid tubercle, behind which is a large foramen, the post-glenoid foramen, for the transmission of the lateral jugular vein. From the region of the post-glenoid tubercle the lower margin of the squamosum arches downwards and backwards behind the tympanic bone and comes to an end below and anterior to the root of the processus styloideus which it consequently overlaps. The lower end of this inferior border is separated from the processus styloideus by the facial nerve which is here hooking around the outer side of the processus styloideus. Beyond this region in a backward direction the inferior border of the bone is sharp and straight and to its whole length is attached the sterno-mastoid muscle. For that reason it may be regarded as a mastoid process, but from its continuity with the squamosum is equally entitled to be called the post auditory process of that bone. The posterior edge of the squamosum is almost vertical and overlaps the anterior edge of the lateral semicircular canal.

The *tympanicum* consists of two parts, viz. the ecto-tympanicum—the tympanic of ordinary terminology—which is a membrane bone, and the endo- or meta-tympanicum which is derived from cartilage and forms the tympanic bulla.

The *ecto-tympanicum* is of much the usual form at such age, is an incomplete ring, open just lateral to the neck of the malleus cartilage and the root of the styloid process. Its upper or anterior limb passes from its commencement behind, forwards along the outer side of the head of the malleus and the root of Meckel's cartilage, on reaching which it sinks under that cartilage and is separated from it by the goniale (prearticular); it then descends to come into medial relation to the processus styloideus, near the ossified part of the latter; it now curves backwards and upwards almost parallel with the processus styloideus and comes to an end just below the commencement of the manubrium mallei and immediately in front of the oblique inner surface of the processus styloideus. In immediate contact with the posterior half of the medial border of the ecto-tympanic is found the *ento-tympanicum*

(meta-tympanicum—Wincza) or tympanic bulla. This is a large curved triangular plate pointed in front, which hides from latero-inferior view the prominentia cochleae and the foramen rotundum, and it supports from below the first pharyngeal pouch which rests upon it, and whose width here is coextensive with the cartilage. Beneath its medial margin (fig. 6) the internal carotid artery, accompanied by branches of the sympathetic, passes upwards along the wall of the cochlear capsule. The most posterior level of the ento-tympanicum as well as of the accompanying first pharyngeal pouch is reached at the chorda-tympani nerve. The cartilage is a very thin plate and is nowhere ossified at this stage, and it is only connected with the ecto-tympanicum by fibrous tissue. Much has been written in regard to the significance from the morphological point of view, and regarding the tympanic bulla in general. To my mind from the fact that it resembles very much in its structure the auricular cartilage, the cartilage of the Eustachian tube and that of the younger nasal cartilages, it seems fair to assume that it is really a provision for support of the outer end of the first pharyngeal pouch more especially protecting it from the pressure of the digastric muscle which at this stage is of large size. The Eustachian cartilage does the same for the aditus of the first pharyngeal pouch. In the case of the ento-tympanicum the cartilage remains of the hyaline type which later becomes bone, the requirements of it being merely that of protection. In the case of the Eustachian tube which subserves an additional function, elastic pores are developed to ensure its pliability. Both cartilages may be taken as primitively of equal morphological value, the Eustachian cartilage being a supporting cartilage to the roof and sides of the aditus of the first pharyngeal pouch, the ento-tympanic cartilage being a support to the outer large end of that pouch, and they both chondrify at the same time in the same strand of connective tissue, viz. the connective tissue which surrounds the first pharyngeal pouch.

The *petrosum*. Much of the auditory capsule has undergone both perichondrial as well as ento-chondral ossification, but as the stain here is not quite as satisfactory as it might be the limits of the ossific centres are not sufficiently easy to describe or model. This is a question which will form the subject of a future communication.

The *zygomaticum* or malar bone is a small rod-like membrane bone developed in the gap between the zygomatic process of the maxilla and that of the squamosum. It overlaps the former on its outer side and is overlapped by the latter from above. So much overlapping occurs that very little of the bone itself is free.

The *post-sphenoid* forms the whole of the floor of the pituitary fossa, extending behind to the root of the dorsum sellae and forwards a little in front of the floor of the pituitary fossa. On each side of the fossa a bony arm is projected transversely which is tipped with cartilage, which comes into contact with the cartilage of the ala temporalis and is only imperfectly fused with it. The stage is too old to determine how this region was originally ossified.

There is no sign of any presphenoidal ossification.

The *occipital ossifications.*

There are present here, a basioccipital, two exoccipitals, and a supra-occipital.

The basioccipital ossification extends from the front of the foramen magnum and a little distance on each side in front of the hypoglossal canals forwards to about the middle of the cochlear capsule. Towards its anterior end this ossific centre appears to be U-shaped in coronal section, extending further forwards below and at the sides of the pars chordalis cartilage than above, hence the cartilage appears here to be lodged in the hollow of the U-shaped bone, the hollow being upwards. The notochord has entirely disappeared in the region of this ossific centre.

Each *exoccipital* centre is here quite independent of the other occipital centres of ossification and commences behind opposite the middle of the lateral wall of the foramen magnum and near the foraminal edge of the cartilage of the exoccipital; later it is seen to be both ento-chondral and peri-chondrial, the latter extending on the medial side almost up to the crus commune of the pars canalicularis of the auditory capsule with which the exoccipital cartilage is fused. Still further forwards this peri-chondrial ossification forms the floor of the medial half of the groove for the lateral sinus, and on the infero-lateral side the cavity of the occipito-atlantal joint is visible, and the ento-chondral centre now is covered below by the articular cartilage of the occipital condyle which is naturally unossified; further forwards this cap of articular cartilage becomes separated from the ossified cartilage by unossified cartilage, and the peri-chondrial bone is now forming the outer part of the exoccipito-capsular fissure, and this it continues to do until the level of the spinal accessory nerve is reached.

Still later, when the lamina alaris becomes evident, peri-chondrial bone spreads under that but not so far as the exoccipito-capsular (supra-alar—Voit) fissure; in fact it reaches to the medial side of insertion of the rectus capitis lateralis muscle. It, on the upper side of the lamina, reaches to the edge of the lateral sinus. The ento-chondral ossification has by now drawn away from the foramen magnum and is concentrated around the hypoglossal canal in its postero-lateral wall, extending somewhat further along the outer side than the inner one. The anterior wall of the hypoglossal canal is quite unossified. The hypoglossal nerve emerges from the canal in two bundles.

The *supraoccipital* is partly peri-chondrial and partly ento-chondral in ossification and formed thus both around and at the expense of the supra-occipital cartilage. At first, that is at its anterior part, it is mainly peri-chondrial and laid down on the caval side of the supraoccipital cartilage along which it reaches to the level of the hind end of the saccus endolymphaticus and by this time much ento-chondral bone has been formed; later peri-chondrial bone reaches to the outer side of the saccus endolymphaticus, but behind this the cartilage rapidly all disappears, having been completely ossified and it is no

longer possible to say where peri-chondrial bone ends and ento-chondral bone begins. At this stage the supraoccipital is a single bone forming a bony tectum posterius and completing the foramen magnum posteriorly.

The *mandible* is a very long bone reaching from the glenoid fossa of the squamosum to the anterior end of the head. Its hind end shows three processes of which the uppermost is the coronoid, the middle the processus condyloideus and the lowest the angular process. Each of these to a large extent consists of cartilage and the cartilage of the angular process is continuous with that of the condyle. In each case the cartilage is elongated in a forward direction and, save at the actual head of the condylar process, is partly ossified. The long axis of the condyle is transverse (fig. 18). Anterior to these three processes the mandible becomes U-shaped, the lateral and medial limbs of the U being the respective alveolar walls anteriorly in relation to the premolar, canine and incisor teeth. Alveolar septa are present so that well-developed tooth-sockets are present. A double mental foramen perforates the lateral alveolar wall not far from the anterior end of the mandible. At the level of the interval between the first and second premolar tooth-sockets Meckel's cartilage which, previously lain along the medial side of the mandible, sinks into the bone and becomes surrounded by a bony tube. It again emerges just in front of the canine tooth-socket and soon fuses with its fellow. The medial alveolar wall just above and anterior to the site of emergence of Meckel's cartilage develops an accessory cartilage (fig. 19) like that which I have described in *Microtus amphibius*. None of these accessory cartilages is ossified independently and all are quite independent of Meckel's cartilage and of much later formation.

REFERENCES

(1) Flower and Lydekker. *Mammals living and extinct.* 1891.
(2) Weber. *Die Säugethiere.* 1904.
(3) Voit. *Das Primordialcranium des Kaninchens-Anat.* Hefte I. Abt. 116? Heft. (38 Bd., 113).
(4) Terry. "The Primordial Cranium of the Cat." *Journal of Morphology,* vol. xxix. No. 2, Sept. 1917.
(5) Fawcett. "The Primordial Cranium of *Erinaceus europæus.*" *Journal of Anatomy,* vol. lii.
(6) Noordenbos, W. "Über die Entwickelung des Chondrocraniums der Säugetiere." *Petrus Camper.* Deel iii. Apl. 3 u. 4.
(7) Fawcett. *Journal of Anatomy,* vol. xlv. 1910–11.

The Os Septo-maxillare of *Tatusia novemcincta*.

This bone, so far as is known, occurs only in Tatusia amongst mammals. Broom (1) first noticed it and Fuchs (2) has given a detailed description of it, and has discussed against Gaupp its morphology. It is not proposed to enter into the question of its morphology here, but merely to describe its position and by a little alteration in terminology perhaps render its understanding somewhat simpler. Two plates are submitted which are drawings of a model made from the snout of a 60 mm. Tatusia embryo given me by Prof. Wood Jones. In Plate XX a ventral view is given and in Plate XXI a left lateral view.

In Plate XX the septo-maxillare is seen lying immediately ventral to the lamina transversalis anterior, and it consists of two parts, one a body the other an anterior ascending process. The anterior ascending process passes forwards and upwards under cover of the naso-lacrimal duct and lateral to the processus lateralis ventralis of the septum nasi to the supero-medial border of the *margino-turbinal*. The central part of the body of the septo-maxillare has been cut out in order to show the lamina transversalis anterior lying deep to it. The body of the septo-maxillary bone is concealed from ventral view partly by the palatine plate of the premaxillary (incisivum) bone and to a large extent by the paraseptal process of that bone. On the right side of Plate XX dotted lines show the course taken by the paraseptal process—a structure which ossifies independently of the rest of the premaxillary bone, and is well marked at the 17 mm. stage when the rest of the bone is absent. Evidently the body of the os septo-maxillare is a covering bone to the lamina transversalis anterior and separates the premaxilla from it. In other mammals known to me the premaxilla takes its place in this respect. The relations of the anterior ascending process are not easily understood until one examines the condition of the nasal capsule. An examination of the lateral wall as presented in Plate XXI shows us that a large somewhat triangular fenestra is present in it which has isolated to a great extent the lateral margin of the anterior narial aperture, and the part isolated in this way has become bent upwards towards the nasal cavity to project therein as a prominent spur to which I have suggested the name margino-turbinal. Some distance above and in front of this margino-turbinal the isolated margin shows the processus alaris superior, whilst below and behind is the processus alaris inferior. The condition recalls that seen in Miniopterus and is due to the same causes. The two principal causes are first the almost complete isolation of the lateral margin of the anterior narial aperture by the development of a large lateral fenestra (which is not present at an earlier period), and secondly the bending out of the nasal mucosa to find a lateral opening. This outward bend of the nasal mucosa (compare Miniopterus, Pl. XVIII) so affects the margin between the superior and inferior alae processes as to produce a bend towards the nasal cavity which develops into a spur along whose medial side the anterior part of the ascending process

of the septo-maxillare lies, but it will be seen that this ascending process is also in relation with another piece of cartilage which in the lateral view through the lateral fenestra appears to project forwards and upwards into the nasal cavity. This cartilage is a spur-like prolongation of the atrio-turbinal which posteriorly is continuous with the maxillo-turbinal. The atrio-turbinal is caused in the usual way, viz. by an upbending of the lamina transversalis anterior over the naso-lacrimal duct into the cavity of the nose. At its free upper extremity it divides into two laminae. Between the margino-turbinale and the atrio-turbinale is a deep incisure which is walled in medially by the anterior ascending process of the septo-maxillare.

In conclusion it may be said that the septo-maxillary bone is a covering bone by its body to the lamina transversalis anterior and by its anterior ascending process to the atrio- and margino-turbinals. As to why it does not occur in other mammals whose nasal apparatus is so similar I do not know.

A cartilaginous septo-turbinal is present at this stage along the dorsal anterior part of the septum nasi.

The expenses incurred by this research were defrayed by a grant from the University Colston Research Society.

RÉFERENCES

(1) Broom, R. *Journ. of Anat. and Physiol.* 1897.
(2) Fuchs, H. *Anat. Anzeiger,* xxxviii. Band. 1911.

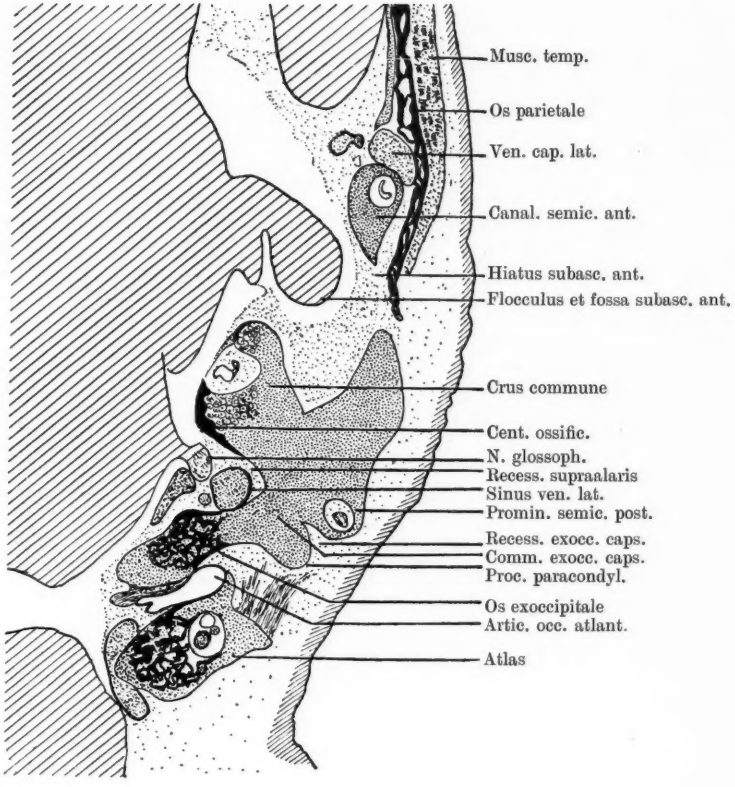


Fig. 1. Coronal section through exoccipital, etc.

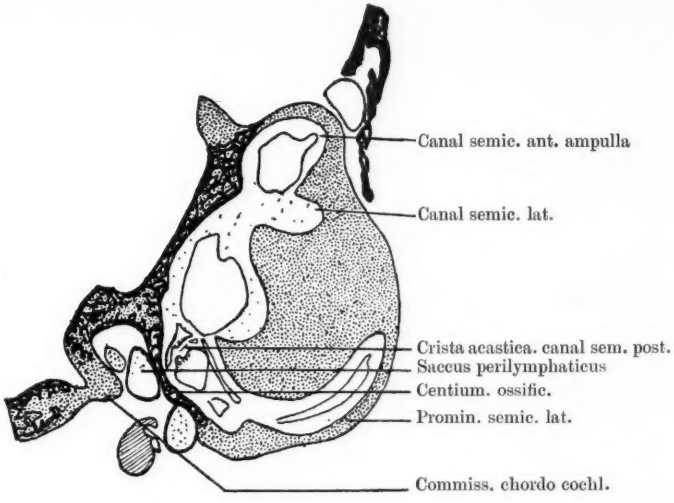


Fig. 2. Coronal section through auditory capsule at level of prominentia semicularis lateralis.

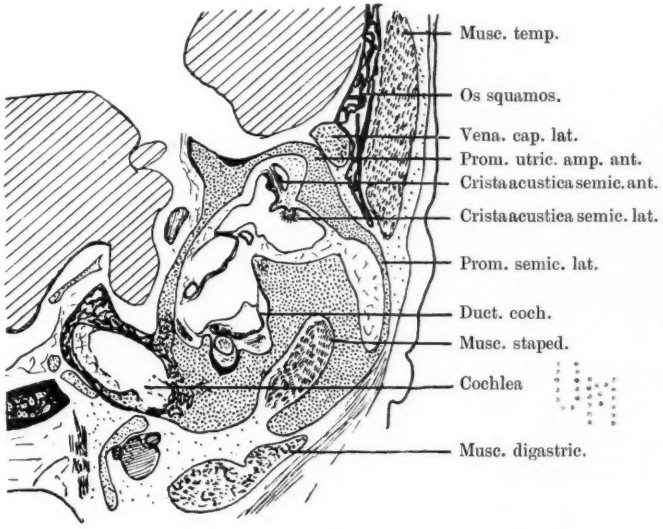


Fig. 3. Coronal section through auditory capsule at fossa musc. stapedii.

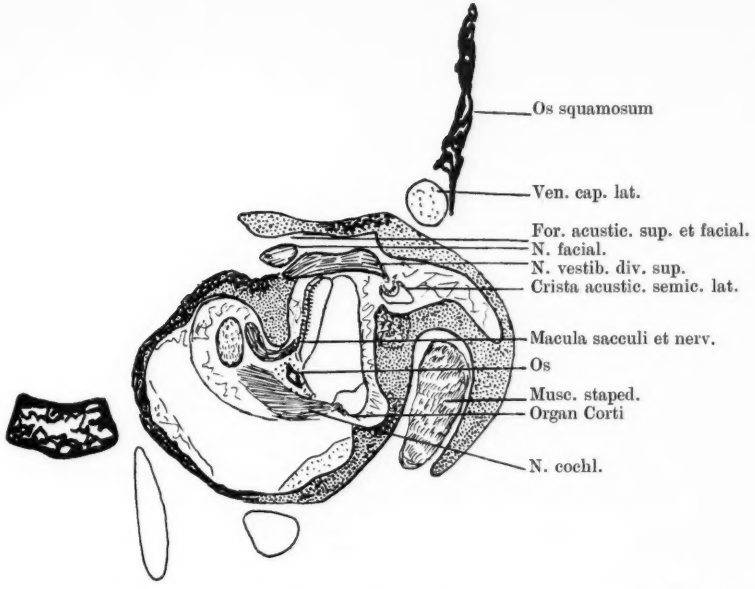


Fig. 4. Coronal section of auditory capsule at level of foramen acusticum superius et faciale.

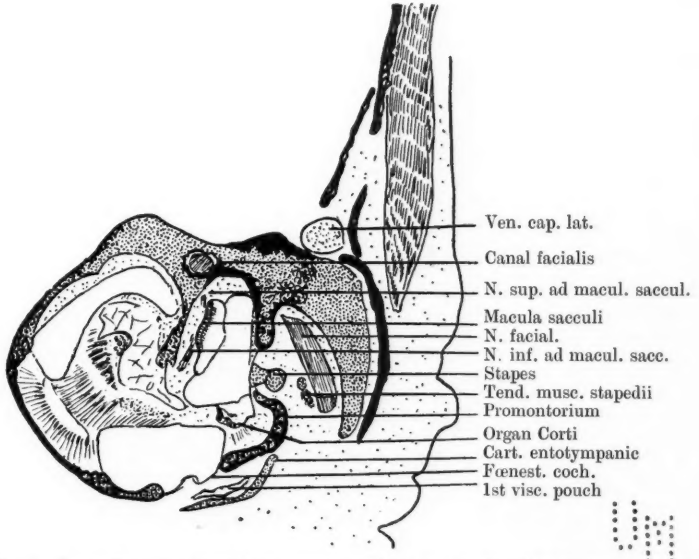


Fig. 5. Coronal section through auditory capsule at level of fœnestive vestibuli et cochleae.

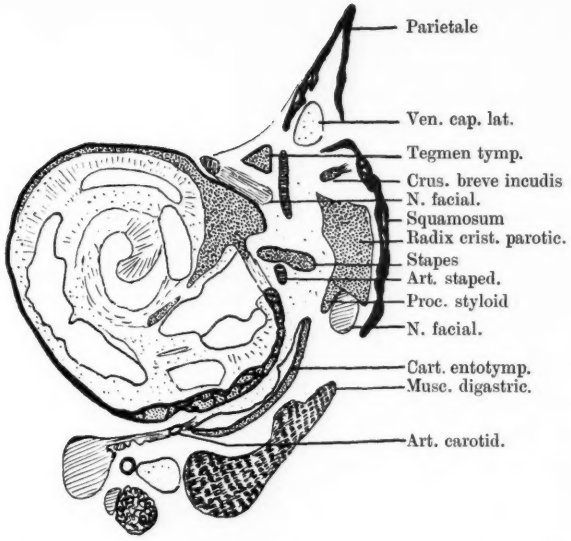


Fig. 6. Coronal section through auditory capsule at level of most fully developed part of entotympanic cartilage which is seen supporting first visceral pouch.

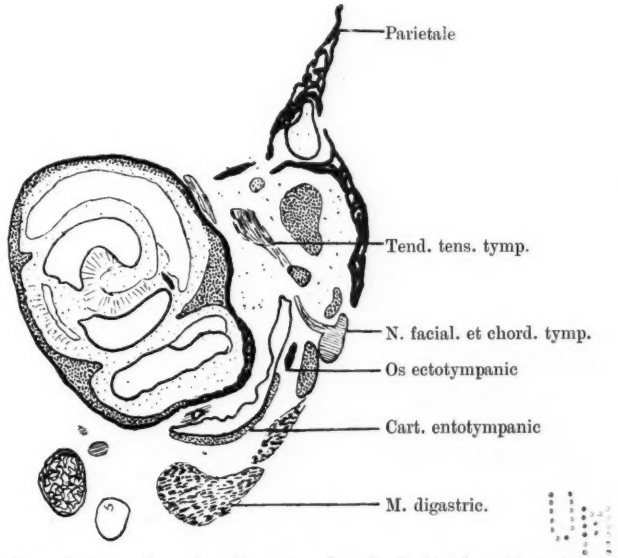


Fig. 7. Coronal section through auditory capsule at level of tendon of insertion of tensor tympani muscle.

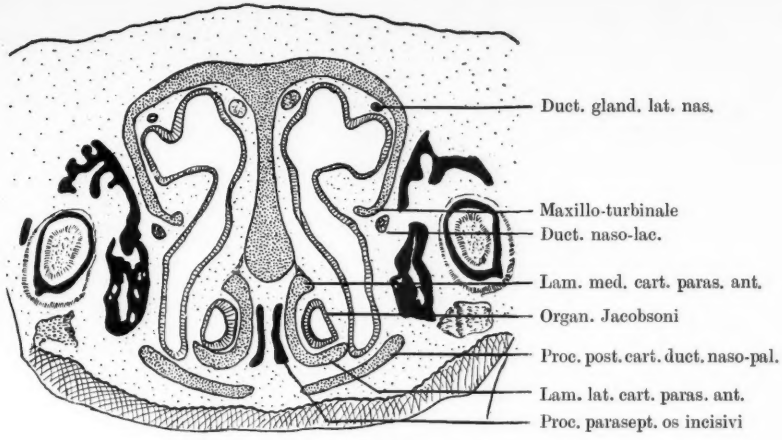


Fig. 8. Coronal section through middle of organ of Jacobson

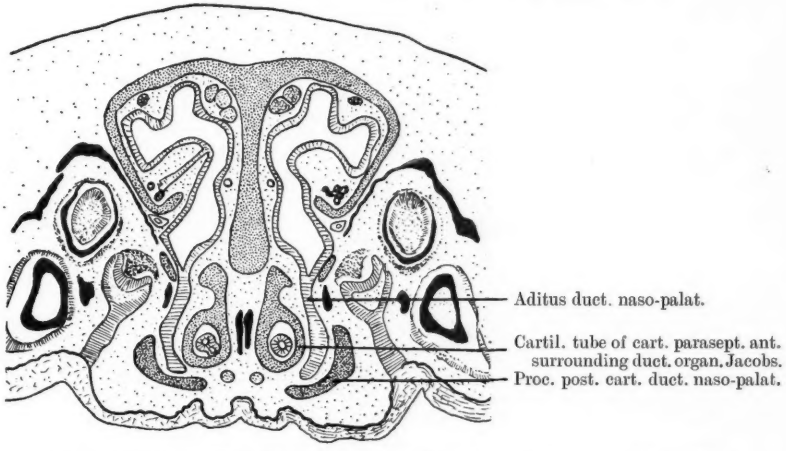


Fig. 9. Coronal section nasal capsule through tunnel in anterior paraseptal cartilage.

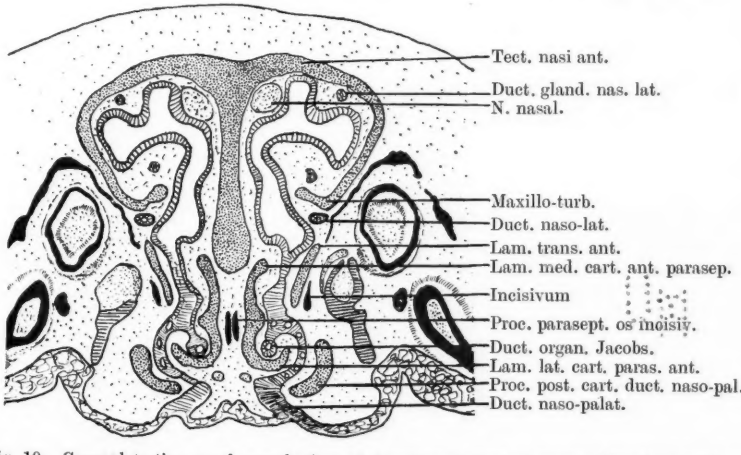


Fig. 10. Coronal section nasal capsule through junction of duct of organ of Jacobson with naso-palatine duct.

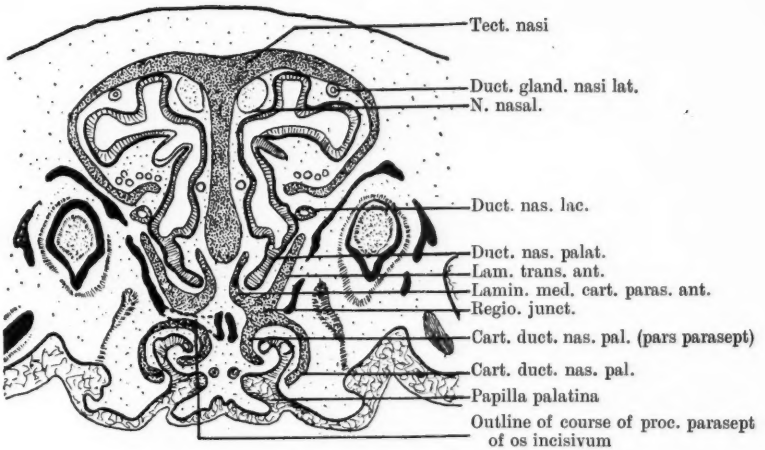


Fig. 11. Coronal section of nasal capsule at level of confluence of lamina transversalis anterior with anterior paraseptive cartilage and cartilage of naso-palatine duct.

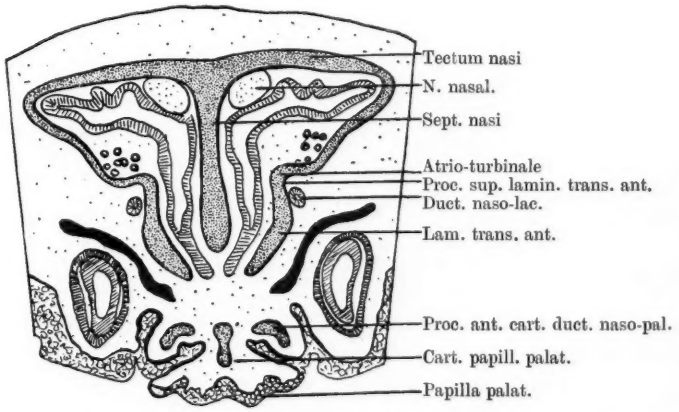


Fig. 12. Coronal section through nasal capsule at level of cartilage of papilla palatina.

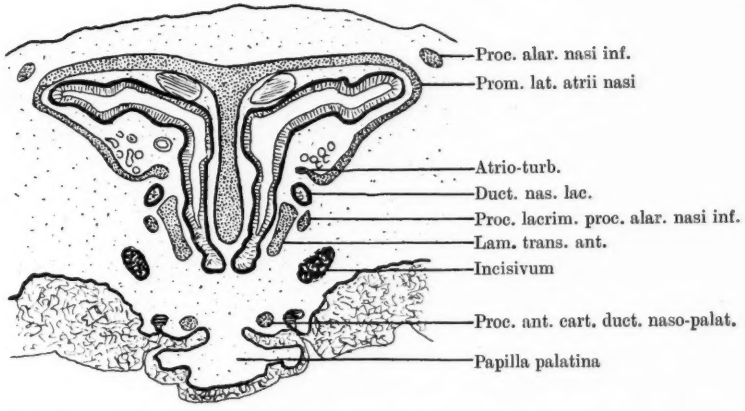


Fig. 13. Coronal section of nasal capsule at level of apex of processus alaris nasi inferior.

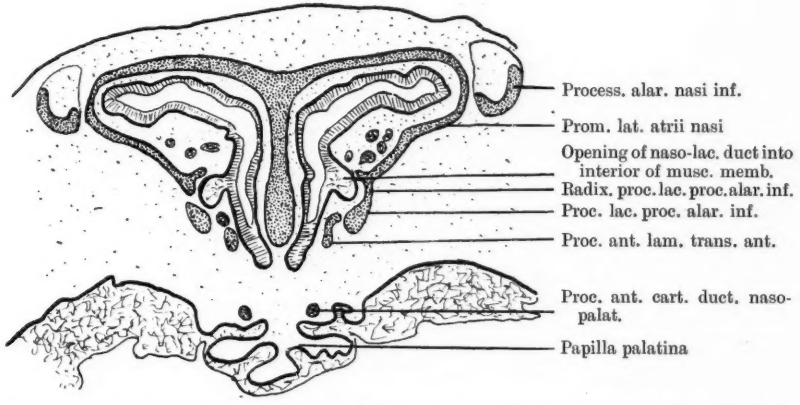

Process. alar. nasi inf.
Prom. lat. atrii nasi
Opening of naso-lac. duct into interior of muse. memb.
Radix. proc. lac. proc. alar. inf.
Proc. lac. proc. alar. inf.
Proc. ant. lam. trans. ant.
Proc. ant. cart. duct. naso-palat.
Papilla palatina

Fig. 14. Coronal section of nasal capsule through root of lacrimal process of processus alaris nasi inferior.

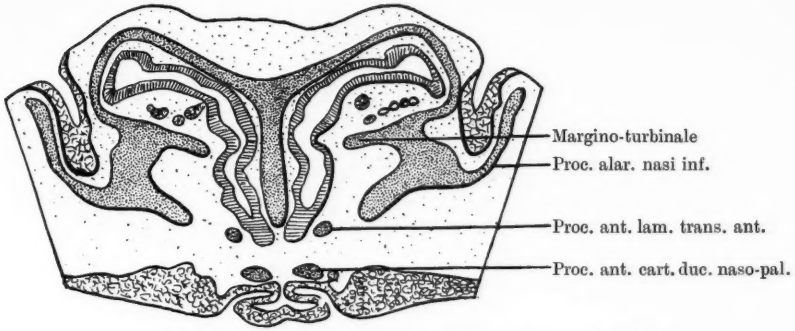


Fig. 15. Coronal section through nasal capsule at margino-turbinale.

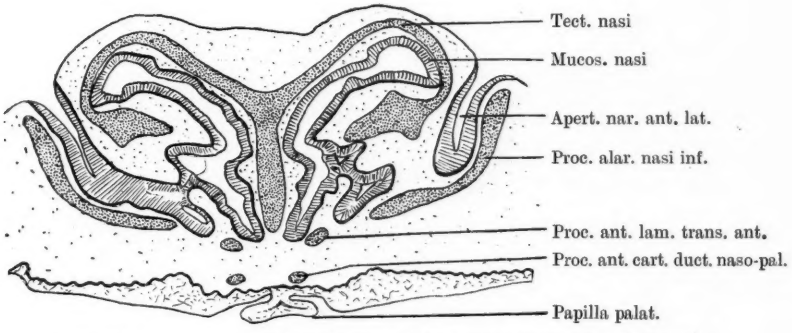


Fig. 16. Coronal section through antero-lateral part of anterior nasial aperture.

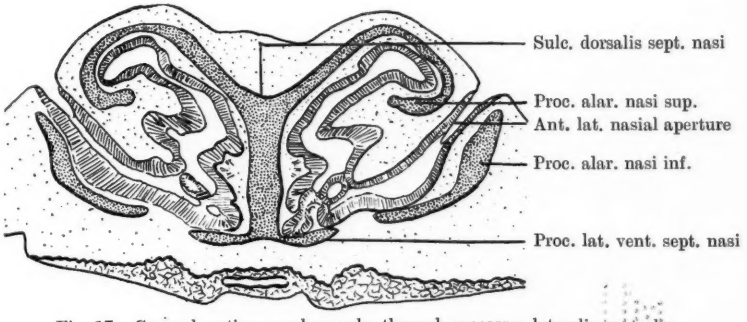


Fig. 17. Coronal section nasal capsule, through processus lateralis ventralis.

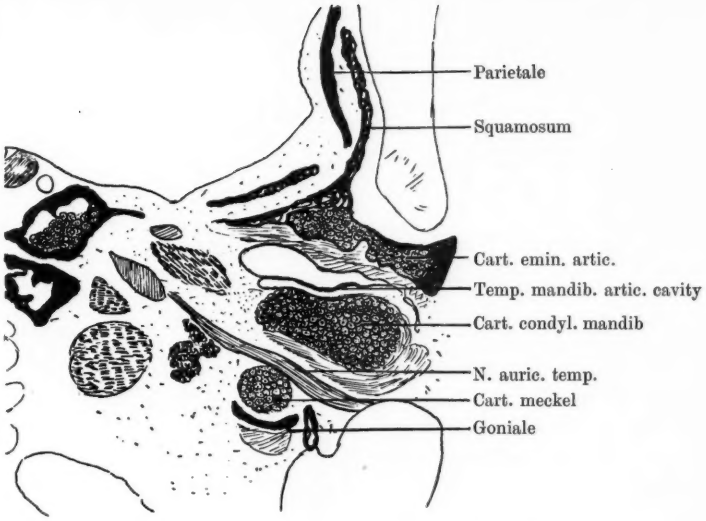


Fig. 18. Coronal section through condyle of mandible etc.

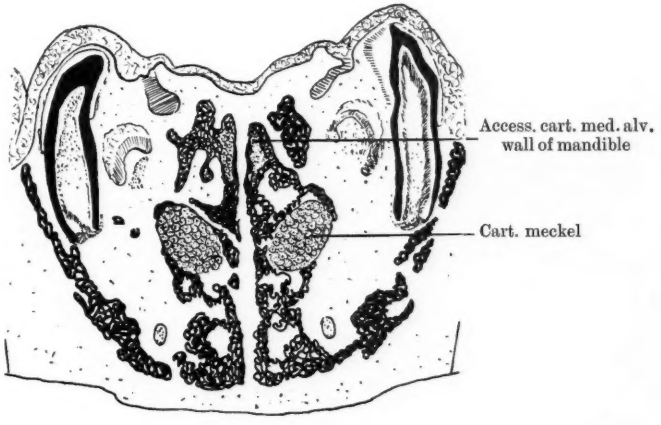


Fig. 19. Coronal section through anterior part of mandible.

MU

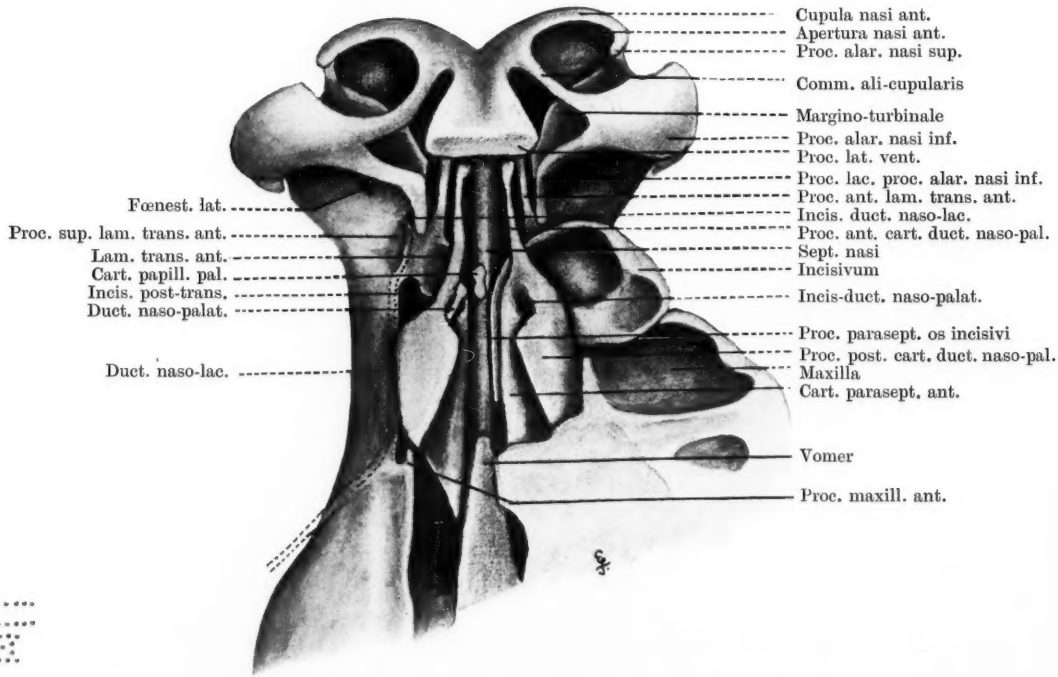


Fig. 20. Ventral view of anterior part of solum nasi and anterior end of nasal capsule.

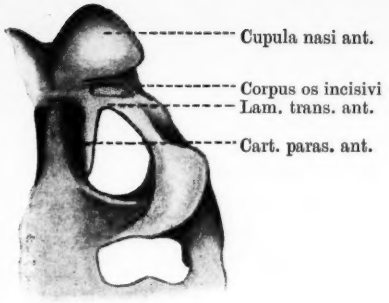


Fig. A. Ventral view solum nasi *Dasyurus viverrinus* at 7 mm. stage.

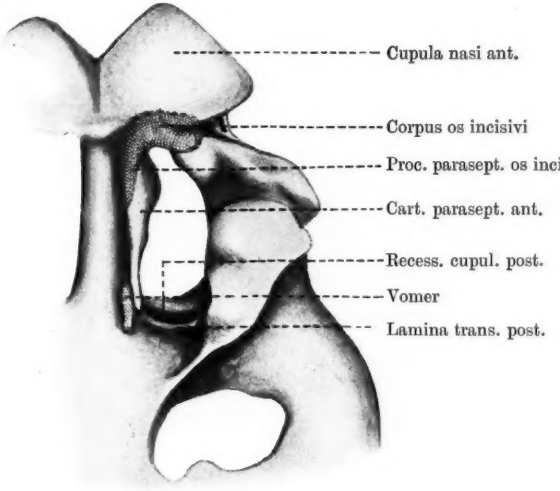


Fig. B. Ventral view of solum nasi of *Dasyurus viverrinus* (Hill embryo). 9·5 mm. stage, total length.

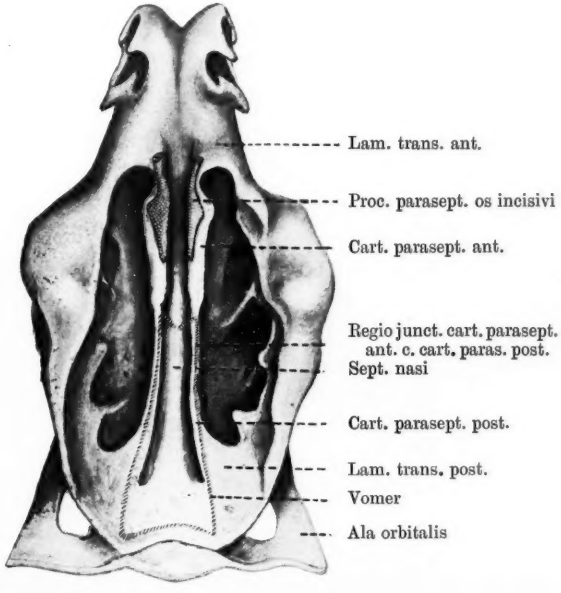
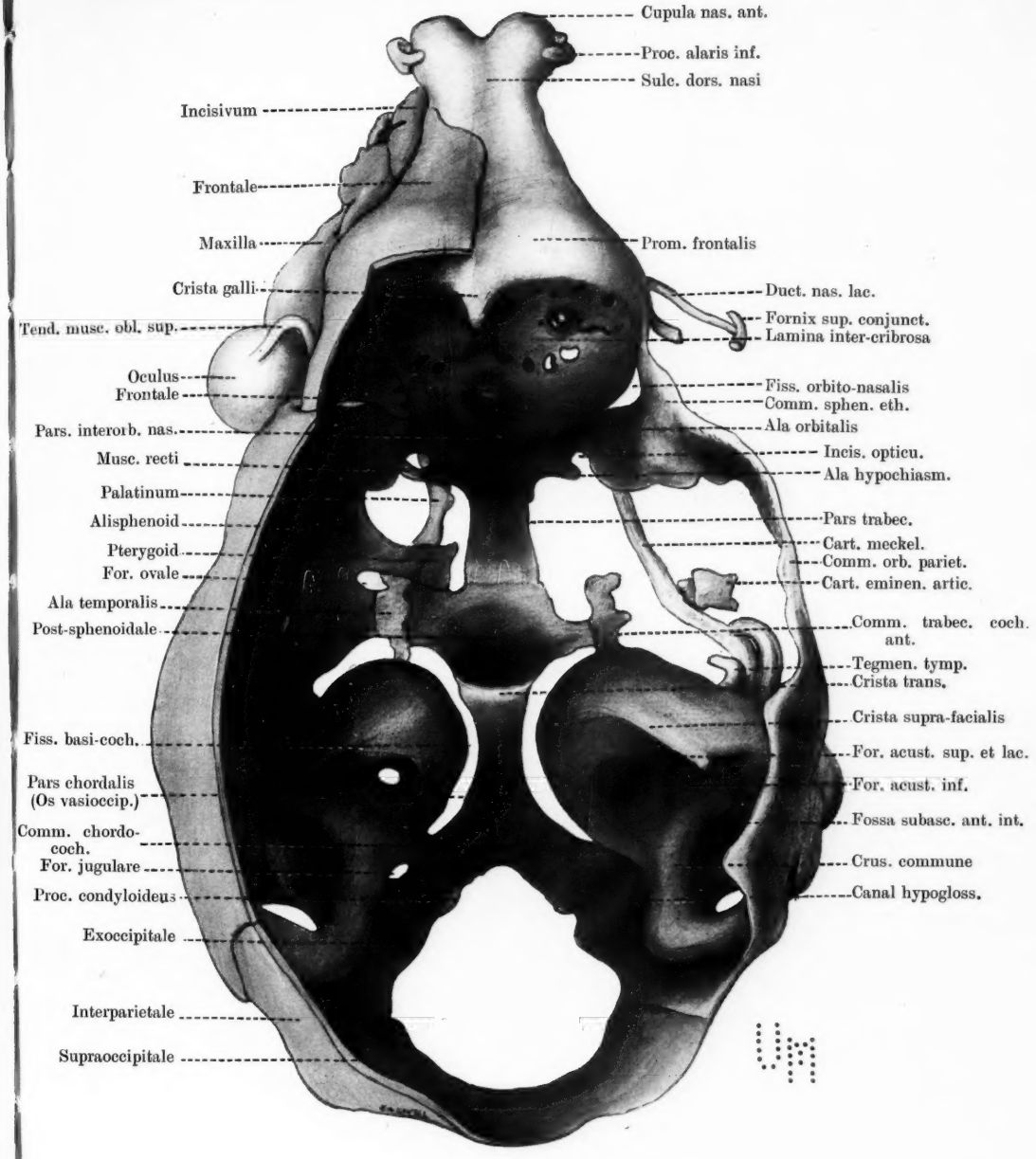
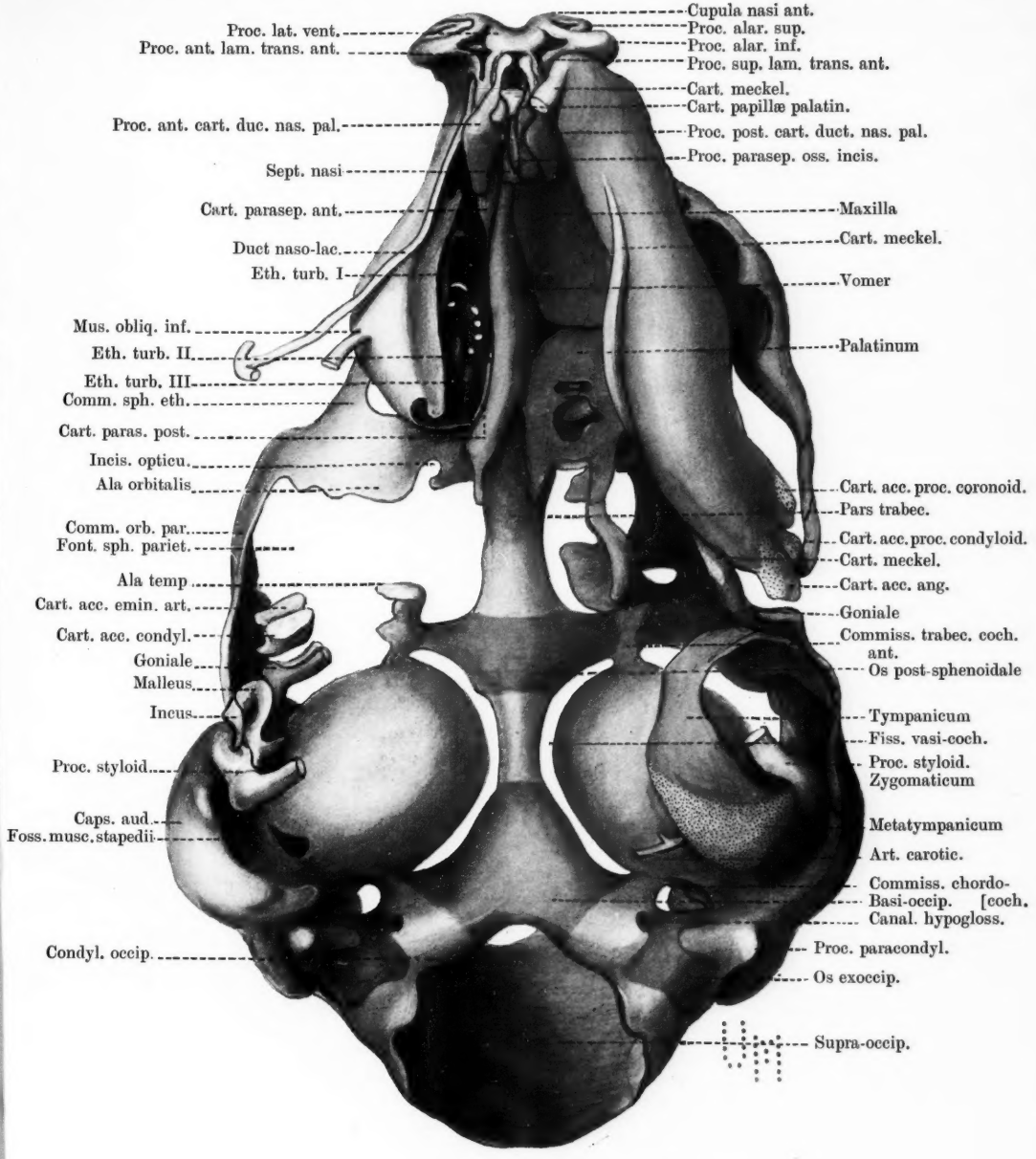


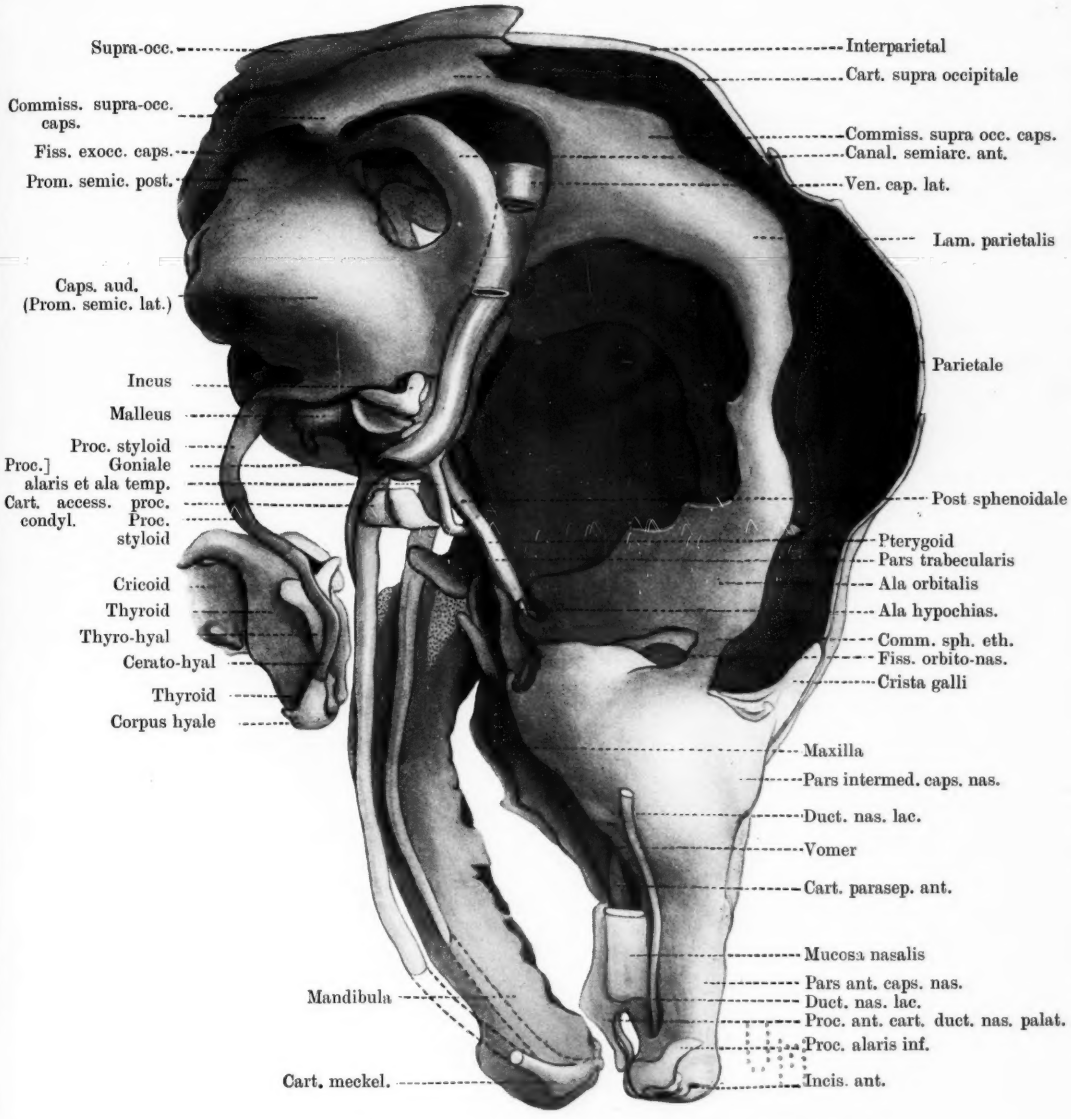
Fig. C. Ventral view solum nasi *Dasyurus viverrinus* (Wood-Jones embryo). 25 mm. stage, total length.



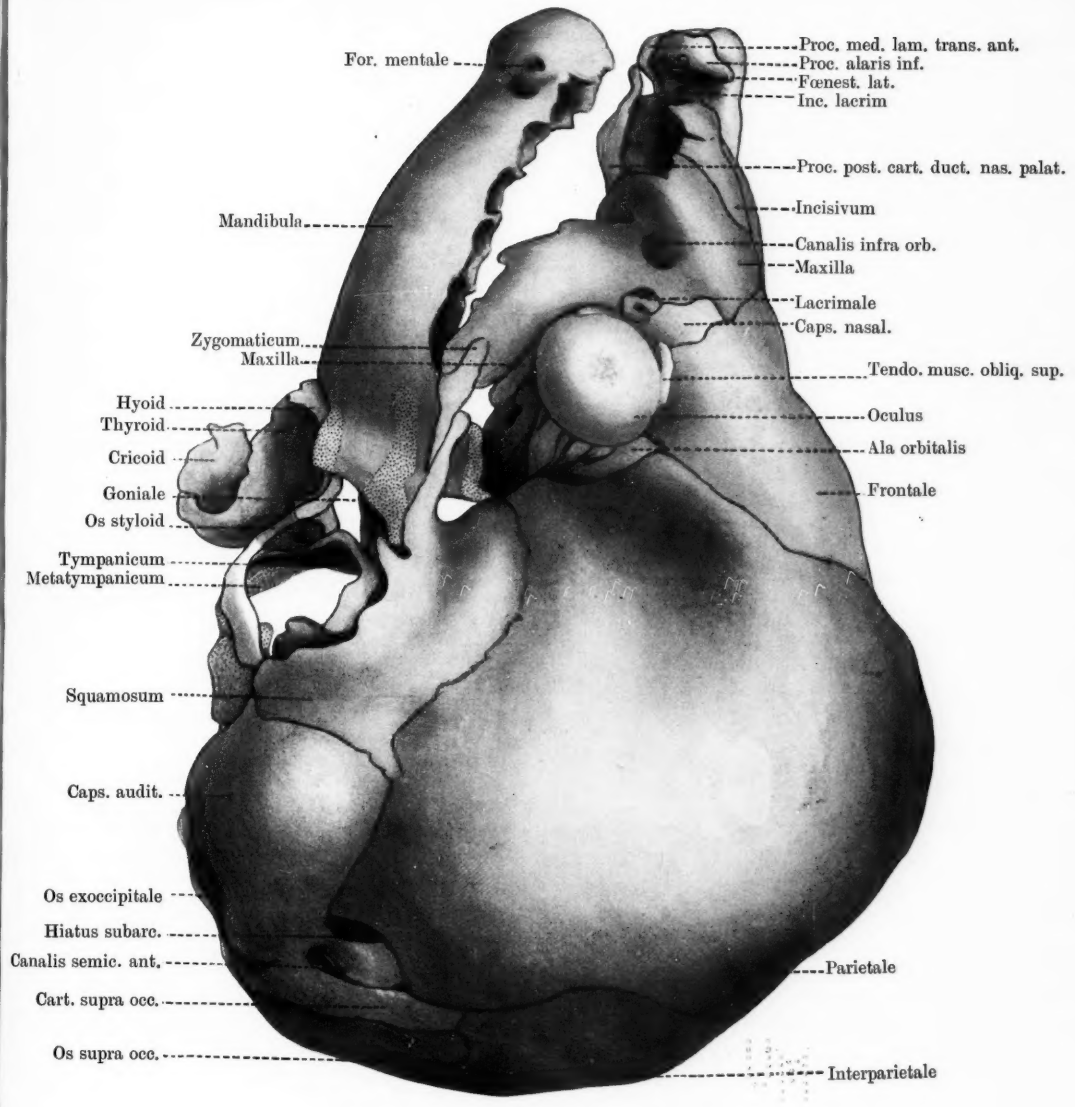
Miniopterus schreibersi. Primordial cranium of 17 mm. (Hill) embryo, from above.



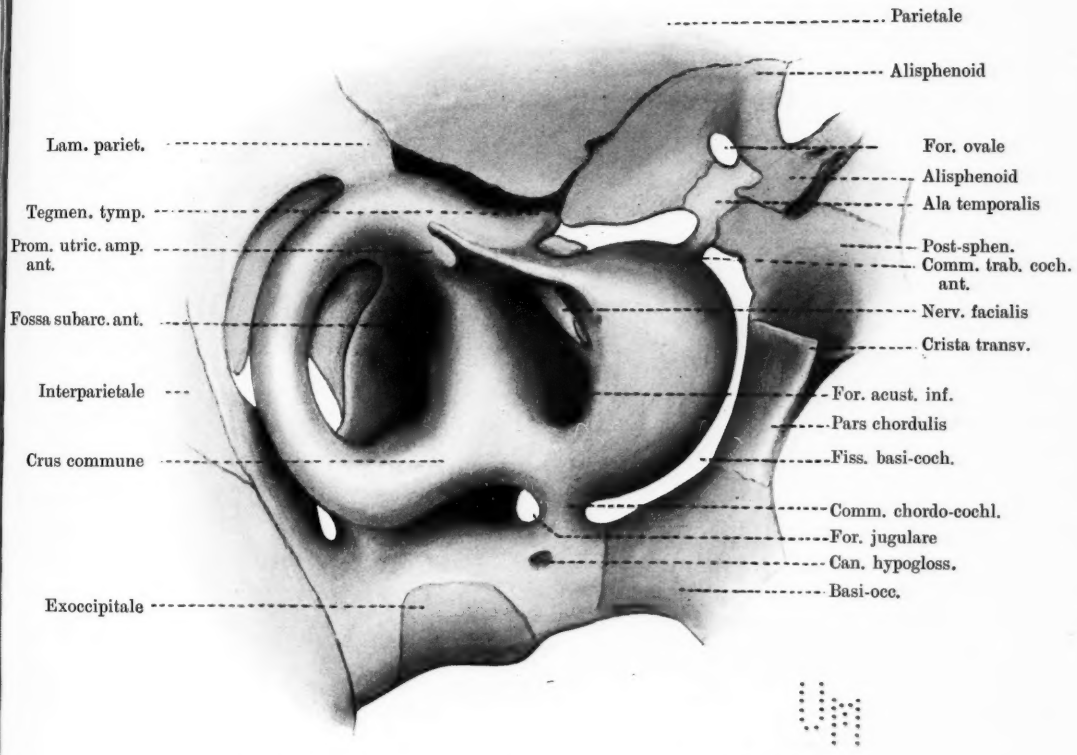
Miniopterus schreibersi. Primordial cranium of 17 mm. (Hill) embryo, from below.



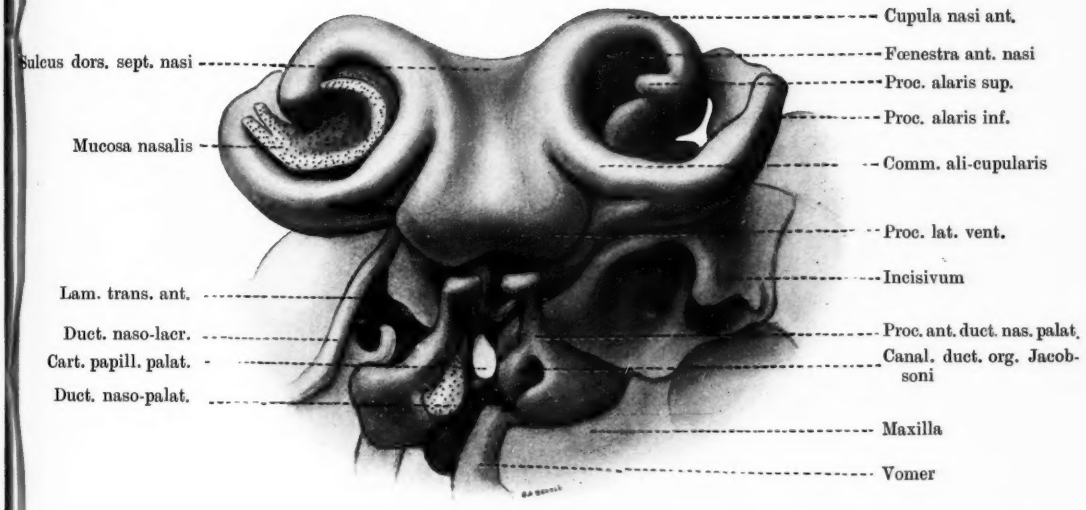
Miniopterus schreibersi. Primordial cranium of 17 mm. (Hill) embryo, from right side.



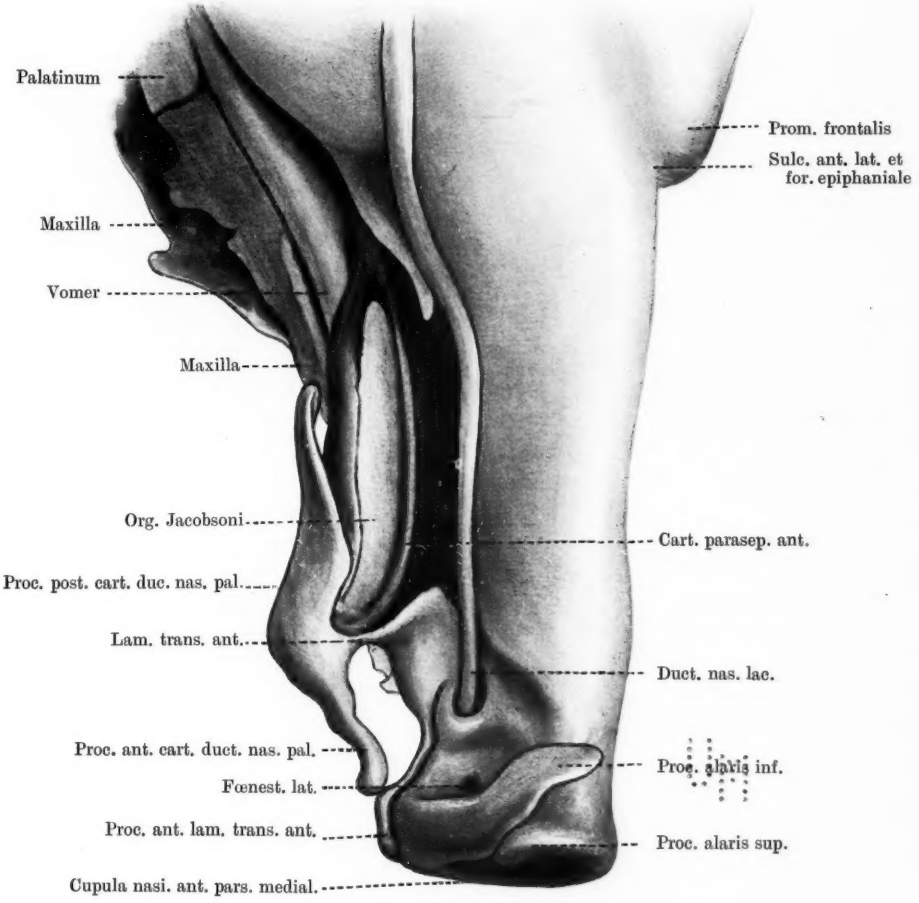
Miniopterus schreibersi. Primordial cranium of 17 mm. (Hill) embryo, from left side.



Miniopterus schreibersi (Hill embryo). Medial aspect of auditory capsule of left side.



Miniopterus schreibersi. Nasal capsule, viewed from front and below.



Miniopterus schreibersi. Nasal capsule, viewed from right side.

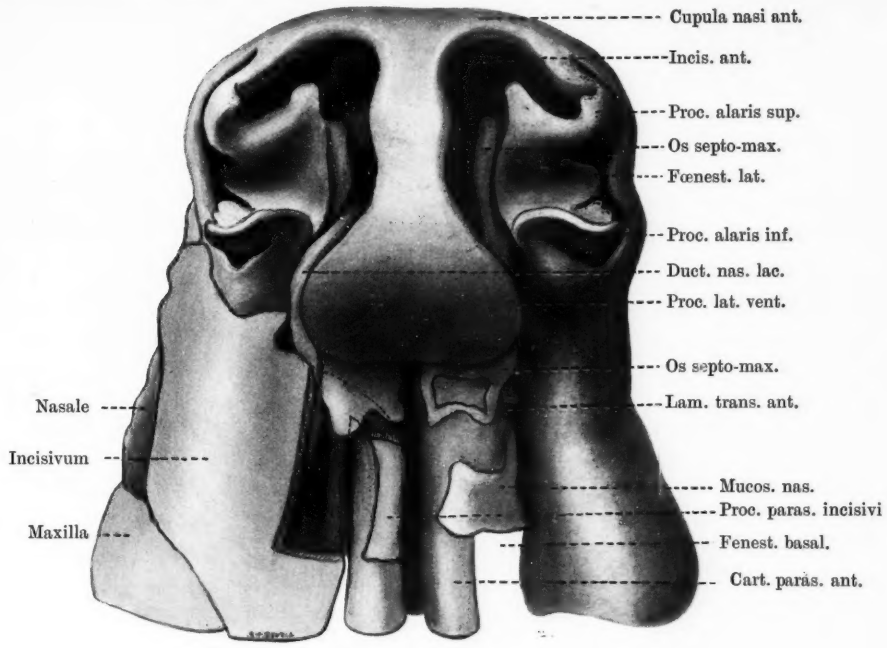


Plate XX. *Tatusia novemcincta.* Nasal capsule, ventral view.

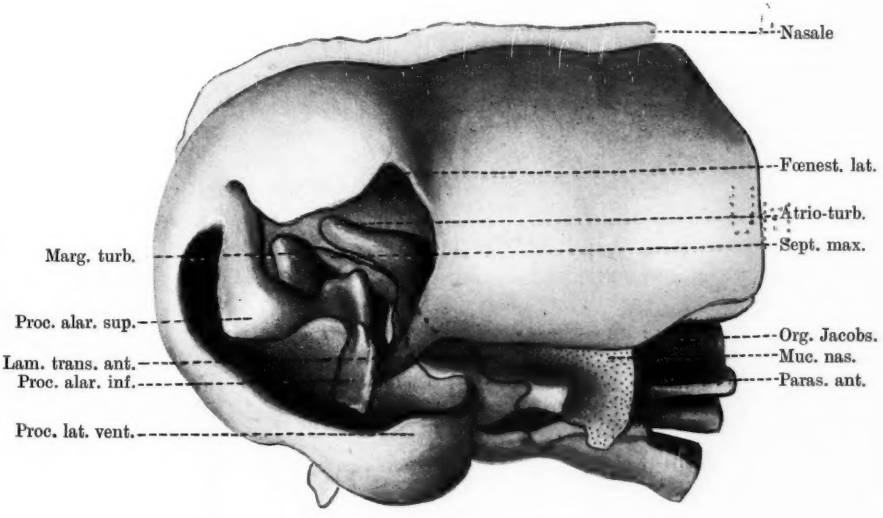


Plate XXI. *Tatusia novemcincta.* Nasal capsule, left lateral view.

THE COMPARATIVE ANATOMY OF THE NUCLEUS AMYGDALAE, THE CLAUSTRUM AND THE INSULAR CORTEX[1]

By PROF. E. LANDAU, M.D.,

Foreign Corresponding Member of the Paris Medico-psychological Society

The material for this research was obtained partly from Professor Monakow's collection in his well-known laboratory in Zurich, and partly from work of my own done in the laboratory of the late Prof. Déjerine during my military service in Paris.

There are not many detailed works in this particular field, and so we will first of all take up minutely each of these cerebral districts.

Let us begin with the *insula.*

The insula (island of Reil) is best developed and most covered in human beings. In man it represents the so-called central lobe of the telencephalon, which lies in the lateral fissure (fissura Sylvii) and is covered as with a lid by parts of the frontal, parietal and temporal lobes. In normally developed human brains the insula is as a rule completely covered, whereas in apes the foremost part is more or less uncovered. In Ungulates the insula is elongated in the fronto-caudal direction: it lies above the rhinal fissure and is only covered in its upper part by the higher gyri. In Carnivores the insula, acording to former authors, is reduced to small proportions. Prof. Moritz Holl, who has for years made a special study of the comparative anatomy of the insula, influenced by Sir William Turner's observation that in the brain of a bear a gyrus lies hidden in the fissura Sylvii, has formed a new theory concerning this part of the brain. R. Anthony has accepted Holl's theory and G. Elliot Smith had independently arrived at a somewhat similar conclusion. According to Holl the insula in human and anthropoid brains is nothing but the first deeply buried arcuate convolution of the Carnivore brain, with its parts in the nasal direction (foremost part of the second arcuate convolution, the lower part of the gyrus orbitalis, the lower part of the gyrus reuniens, that is, the whole convolution district from the lower end of the front part of the first arched convolution to the pre-sylvian fissure). By this assumption Holl ignores the cyto- and fibre-arrangements of the corresponding parts of the cortex in different species. This is, however, refuted by Ernst de Vries. Holl also ignores the fact that the human embryonic insula is quite smooth, and

[1] A lecture delivered to the Natural History Society (Berne) on the 30th November, 1918.

later on becomes folded, which according to Retzius would not be the case if Holl's hypothesis were correct. Kohlbrugge refutes Holl's theory on the ground that the so-called Sylvian fissure autorum appears first in the embryonic brain of Carnivora and therefore should correspond to the Sylvian fissure of man. Holl bases his theory principally on the relations which exist between the island and the claustrum, a small stratum of gray matter which lies near

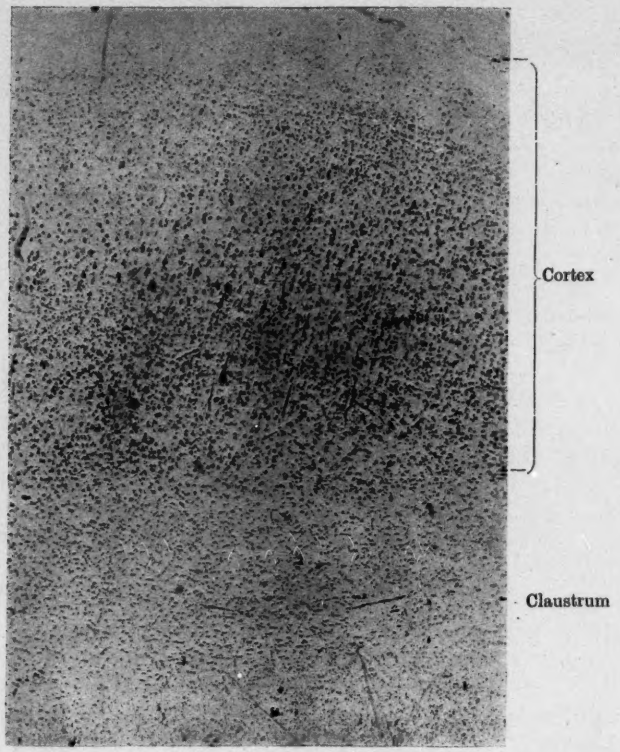


Fig. 1. Cortex insulae (Macacus rhesus). (From a preparation of Prof. C. Monakow's.) A well-formed cortex with the usual strata. The claustrum lies to the side and has no connection with the cortex.

the cortex of the island and is divided from the latter by the capsula extrema. Arguing from these facts Holl considers the whole brain district of Carnivora corresponding to the claustrum as corresponding to the human island. Original as this theory is, we shall take it cautiously as far as Carnivora are concerned, for as Holl admits himself, in these animals the claustrum extends downwards past the rhinal fissure in the lateral district of the rhinencephalon and on the other hand the claustrum of the Carnivora corresponds partially

to a cortex with Betz giant pyramids, which is not the case with the human insula. Some authors (such as Meynert, Wernicke, and lately Brodmann) consider the claustrum as a mass separated from the island cortex; and Brodmann goes so far as to say that he considers the claustrum as the innermost stratum of the island cortex. That this is not the case, and that the claustrum is absolutely independent of the insula we shall soon see. The microscopic structure of the insular cortex too shows that it is in the main no different from other well formed parts of the cerebral cortex, so that the only corresponding characteristic for the insula is its covered position, which in all probability is mechanically formed by a progressive growth of the cerebral hemisphere; the parts which lie against the basal ganglia of the cerebral hemisphere cannot follow this growth and becomes overgrown by the neighbouring parts, and finally completely covered. Now about the *claustrum*, let us cite the following remarks. Basing his opinion probably on the relation of the developed human brain Elliot Smith expresses the following view on this matter. This is a thin plate of gray substance embedded in the white matter which intervenes between the lentiform nucleus and the gray cortex of the insula. Followed in an upward direction it becomes gradually thinner and ultimately disappears. Downwards it thickens considerably and at the base of the brain it comes to the surface at the anterior perforated substance and becomes continuous with the gray matter of the cortex. He emphasises that the extent of the claustrum corresponds very closely to the area occupied by the insula.

Now, if we wanted to accept Brodmann's view that would be easy to explain, for according to him the claustrum forms a stratum separated by the capsula extrema from the island cortex, which in its embryonic state is still connected with the latter. This, however, is not the case. The hypothesis that the claustrum must be considered as belonging to the insula, has also been held by Wernicke, who bases this idea on the fact that the histological elements of the claustrum are nervous, exquisite cells. For present day science this one fact is not sufficient to justify such a conclusion, and we know that formerly the same observation brought Luys to a totally different conjecture, for he says: "L'avant-mûr qui parait de même nature que celle du corps strié...." Luys's idea, however, contradicts the observations by de Vries whom we have to thank for a very interesting study on "The origin of the claustrum." The following is a resumé of this work: The claustrum of higher mammals is represented by an independent gray matter, which is not connected with the cortex, or at least only in its ventral parts, at the passage from the neo-cortex to the lateral olfactory cortex. In many animals (man, gorilla, baboon, elephant, cattle, porpoise, dog and puma) the claustrum lies absolutely separated from the cortex, and does not touch it in any place. Where there was embryological material on this subject (man) it showed that the claustrum was not connected in any way with the cortex. In another place we find the same author makes the following important remarks: "The

lower mammals show with regard to the claustrum a more primitive condition, and we see in Insectivora that the claustrum is formed by an independent development of these zones in the neo-cortical stratum, which borders on the lateral wall of the hemisphere direct on the rhinencephalon."

As we see there is nothing in this statement which coincides with Brodmann's view that the claustrum forms a part of the island cortex separated by the capsula extrema, and which according to this author is connected in

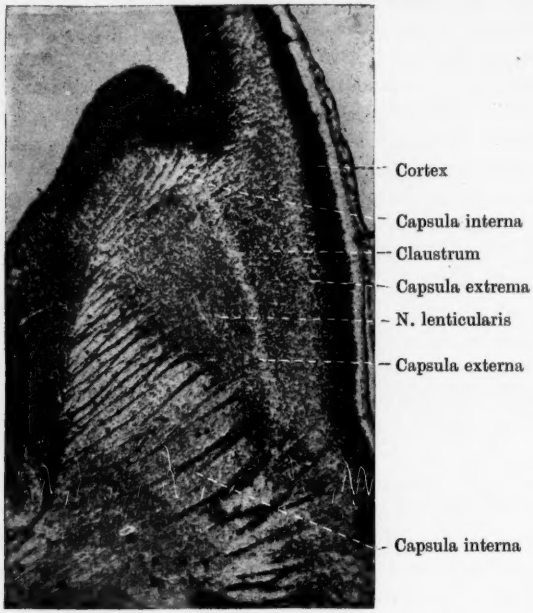


Fig. 2. Horizontal section through an embryonic human brain. 4 cm. long. (From Prof. Monakow's collection.) Here can be seen the capsula interna which is very broad: a part of the nucleus lentiformis, a well-formed claustrum and a cortex with the layers not yet developed.

the embryological state with the island-cortex. It is not very clear how Brodmann could come to such a conclusion, for we can see from microscopic preparations, on the one hand the island cortex differs in no way from other well-developed parts of the cortex of the hemisphere, on the other hand the claustrum shows so many peculiarities that it seems quite impossible to designate this gray substance as a separated innermost stratum of the island cortex.

In a former communication I called attention to the fact that in the brain of an adult a continuous claustrum is not by any means to be seen in all

sections through the island. Here and there the gray matter is interrupted by a mass of the fasciculus uncinatus, and on the latero-basal parts of the nucleus lentiformis it is frayed, as we find very well illustrated in Gray's text-book on anatomy. On the other hand if we look at horizontal sections through the brain, we get the impression that the claustrum belongs to the island cortex, as the capsula externa is uninterrupted and thin, the claustrum itself uniform and narrow. If we examine, however, a deeper section at a height where one can, for instance, see the two corpora geniculata and at the same time the red nucleus of B. Stilling, the commissura anterior and the ansa peduncularis, the claustrum appears much broader and more irregular, and what is most important it is in the middle part completely interrupted by the bundles of the fasciculus uncinatus, so that on the corresponding internal parts of the island cortex there is no claustrum. Now I want to ask if it is right to maintain the hypothesis that a foreign system of association fibres appears between the cell layers of the cortex, which would be the case if Brodmann's interpretation of the claustrum were right. In my opinion that is not very probable. I may also add the following facts to these observations on the brains of adults which have been seen on the brains of animals and embryonic brains. Regarding Carnivore and Ungulate brains we can confirm Holl's opinion that the claustrum in the downward direction crosses the fissura rhinalis and extends to the lateral part of the rhinencephalon. We have found the same thing in the brain of apes (such as Macacus rhesus). On the upper part of the insula in the macaque's brain the claustrum is very narrow, between the capsula extrema and the capsula externa the claustrum follows a small line just at the turning of the island cortex to the cortex of the operculum parietale; in a downward direction the claustrum becomes gradually thicker and then ends in a thick bulb, between the island cortex and the operculum temporale on the one side, and in this case the commissura anterior. The close connection between the lower part of the claustrum with the amygdala, of which we will speak later, is opposed to the theory that the claustrum is the innermost strata of the island cortex.

The most instructive and most important discoveries are, however, those which have been made on embryonic human material. For this purpose I examined two series. One from a foetus 4 cm. long, the other from a child prematurely born at the sixth month. In both cases the cortex is still relatively narrow and not developed in layers, the claustrum on the other hand, which lies far from the cortex in an inward direction has already taken on quite important dimensions. I should also mention that the observations of Voelsch on the brain of a weasel and of de Vries on different brains concerning the projection of the lower part of the claustrum towards the olfactory lobe, I have been able to confirm on sections from the brains of an ape (Hapale).

According to J. Kööiger the name amygdala or nucleus amygdalae defines a thick gray substance underneath the hinder part of the nucleus lentiformis, which occupies the point of the cornu inferius and turns round as a

large globe to the cornu Ammons in the cornu inferius. On three sides, medial, ventral and lateral, the gray substance of this globe is surrounded by a white matter and is only connected on the dorsal and medial side with the cortex of the point of the under lobe.

This last observation that the amygdala on the dorso-medial side is connected with the cortex is explained by some other authors, such as Rauber-Kopsch and Obersteiner, by the claim that the amygdala is nothing else but a swelling of the cortex on the temporal lobe. Obersteiner makes the following statement on this subject: In the nucleus amygdalae underneath the gyrus

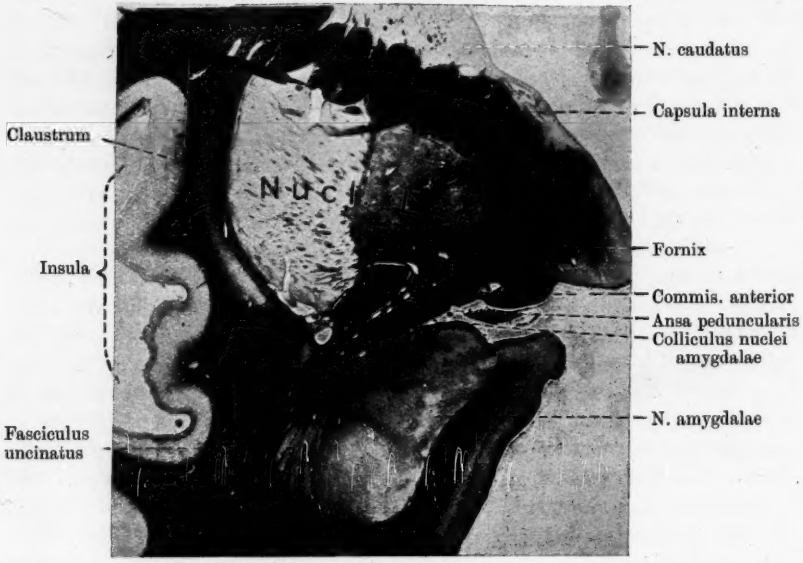


Fig. 3. Frontal section through the brain of an adult man. Here is the whole insular cortex but one can also see that the claustrum exists only in the upper half of the island, just as high as the putamen. In the lower part of the island we see instead of the claustrum the fasciculus uncinatus. The nucleus amygdalae is cut at a point where the ansa peduncularis joins it. It is also interesting to note its connection with the cortex.

uncinatus we find cellular elements similar to those in the cerebral cortex; most of the irregular nerve cells which are scattered here tend to assume a pyramidal form; and Obersteiner is sure that the nucleus amygdalae represents a modified, thickened part of the temporal cortex. As we shall soon see this idea of Obersteiner's is not at all accurate, for on a closer examination of the base of the brain, it is seen that the relation of the nucleus amygdalae to the lateral wall of the hemisphere is similar to that which exists between the head of the corpus striatum and the lateral cerebral wall. It is well known that a certain part of the head of the nucleus caudatus corresponds to the sustantia

perforata anterior and can be examined directly upon the base of a complete human brain. It is described by Déjerine as colliculus nuclei caudati. It is the same with the nucleus amygdala; it does not form simply a thickened part of the corresponding cerebral surface inwardly, but it develops also into a projection, a colliculus, which we, as Elliot Smith shows, can perceive not only on the base of a rabbit's cerebrum, but also on that of a human brain. In the brain of an adult human being this nucleus has altered its position, and we don't find it on the inferior but on the dorso-medial side of the frontal end of the temporal lobe. The "colliculus" of the nucleus amygdala is not found in the field of the substantia perforata anterior in the real sense of the word, but in the province of the lobus piriformis. The latter, however, as the back part of Turner's rhinencephalon, is, in human beings and anthropoid apes, no longer upon the basal surface, as in other animals, but is linked to the medio-dorsal part of the temporal lobe, and is there to be seen in the form of a small projection. The boundary between it and the piriform cortex forms the amygdalian fissure of B. G. Wilder. In embryonic human brains the continuation of the olfactory brain across the lower part of the insula as far as the temporal lobe, can be seen so well in the excellent works of Professor G. Retzius; this part of the human brain corresponds to the piriform area of animals' brains. Just as is seen in the piriform area of animals' brains so also we see on the corresponding part of human brains two projections, the inner described by Retzius as gyrus lunaris, the outer as gyrus ambiens. Now we may say that the gyrus lunaris of Retzius, as can easily be seen from sections, is simply what I call the "colliculus nuclei amygdalae"; and as we should not think of inferring that the nucleus caudatus because of the colliculus nuclei caudati was autogenetically a thickened part of the substantia perforata anterior we have just as little reason to suppose that the amygdala because of its colliculus is a thickened part of the olfactory cortex (see fig. 553 by G. Elliot Smith in Cunningham's *Text-book of Anatomy*, IV. ed. 1917). The attempts of Obersteiner to bring this phylogenetically old formation into close connection with the totally different human temporal cortex is very risky.

As regards the connection of the nucleus amygdalae with the cerebral cortex, we confirm that such really exists. As I showed at the tenth meeting of Swiss Neurologists there exists a direct communieation from the nucleus amygdalae elements to the hippocampal formation. And so we see that on the one hand the internal stratum of nerve cells of the neo-cortex is a continuation of the hippocampal cells, on the other hand the latter are connected with the cells of the nucleus amygdalae. If we follow the line of observation taken up by Campbell, Ariens-Kappers, F. W. Mott, and Elliot Smith we can identify the nucleus amygdalae with the secondary epistriatum of birds. In this way we get a whole chain of interesting phylogenetic facts from the corpus striatum to the secondary epistriatum (the nucleus amygdalae) and from there to the hippocampal formation, to arrive finally at the internal layers

of nerve cells. One can see in certain sagittal sections a streak of gray matter which partially touches the outer side of the nucleus amygdalae and partially connects the cerebral cortex with the substantia perforata anterior.

The internal structure of the nucleus amygdalae is much more complicated than the exterior. In a comparative anatomical study Voelsch has examined the cytoarchitectural structure of this nucleus. He has succeeded in differentiating a number of constant cell groups. These groups consist of small and of large cells, which together form the nucleus amygdalae. Unfortunately I have not suitable material at hand to be able to test this interesting and important theory.

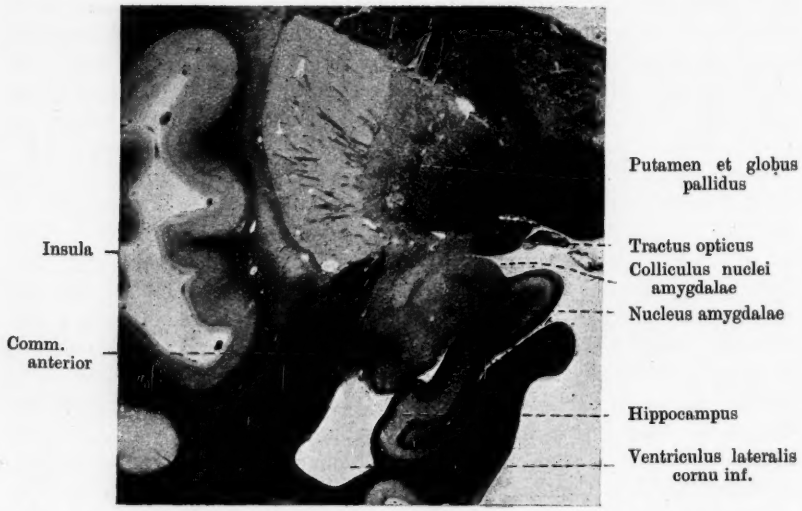


Fig. 4. Frontal section through the brain of an adult man, a little further back than Fig. 3. The close connection between the nucleus amygdalae and the corpus striatum is well seen here; the connection between the amygdala and the cortex is interesting; it is a long sinuous line towards the ventricle, which cytoarchitecturally consists of hippocampal cells.

However, with regard to the claustrum and amygdala Voelsch expresses an opinion with which I cannot agree. He says: "As to the development of the amygdala complex I believe I am able to prove in the mouse that the group of middle-sized cells is to be considered as a sinking in of the superficial cells of the pars intermedia of the piriform area.... I must, in the controversy concerning the character of the claustrum, take sides with those who deny that it belongs to the corpus striatum and who regard it as a separated part of the multiform layer of the cortex. In my opinion there does not exist any connection with the nucleus amygdalae." So much for Voelsch. I think I have explained clearly enough why I do not agree with him.

RÉSUMÉ

Holl's theory that the insula in human and anthropoid brains is nothing but the first deeply buried arcuate convolution of the carnivore brain with its extension in the nasal direction, lacks adequate proof. Holl's opinion is based principally on the theory that between the limits of the insula and the extent of the claustrum there is a complete parallel, but this opinion is not quite free from objection. As I have already said the claustrum in human beings extends considerably beyond the upper limit of the insula (see also fig. 570 in Cunningham's *Text-book of Anatomy*, 1917). In man, the apes and Carnivores the claustrum extends beyond the lower limit of the insula. Besides in carnivorous animals (for instance, in Felis) we find in the cortex which covers the claustrum a part of the cerebral cortex containing giant pyramids of Betz, which, as is well-known, is not found in human beings. So from this standpoint too the theory of Holl must be questioned.

In opposition to Brodmann's claim that the claustrum is an integral part of the insular cortex I must make the following objections:

1. The insular cortex shows, according to Campbell's researches as well as my own observations, a type of complete cell lamination without reckoning the claustrum.

2. In the embryonic state the innermost layer of the insular cortex is never connected with the claustrum. On the contrary, my researches reveal the fact that the embryonic claustrum lies farther from the innermost layer of the island cortex than it does in the adult.

3. The insular cortex is separated from the claustrum not only by the capsula extrema, but also in some parts by the fasciculus uncinatus.

My observations lead me to regard the claustrum as an independent formation which is neither split off from the insular cortex nor from the striatum. It is an independent nucleus of gray matter which is *sui generis* and belongs as much to the basal ganglia as the nucleus caudatus, the nucleus lentiformis and the amygdaloid nucleus do.

The claustrum shows connections with the nucleus amygdalae and the substantia perforata anterior. In a series of sections of a Hapale brain I saw a deep descent of the claustrum in the rhinencephalic cortex so that internally the olfactory cortex directly touches the claustrum.

Nothing can be said with assurance about the function of the claustrum. It is interesting to notice that even those who have made a study of the matter and who deny a connection between the claustrum and the amygdala think it probable that at least a part of the claustrum has the same function as the nucleus amygdalae.

The nucleus amygdalae, which is connected with the claustrum, the striatum and the substantia perforata anterior, forms on the basal aspect of the hemisphere a large gray nucleus, which from its position belongs to the forebrain basal ganglia. Monakow and Elliot Smith are of this opinion. It is

certainly wrong to consider the nucleus amygdalae as a modified thickened part of the temporal cortex, as Obersteiner does, for

I. An amygdaloid nucleus can be seen in rabbits and also in geese where there is no trace of a delimited area homologous with the temporal lobes.

II. The amygdaloid nucleus, according to Elliot Smith's and my own observations, stands in relation to the piriform lobe, and not to the temporal lobe. The amygdaloid nucleus is in connection with what I call the "internal stratum" of the cortex (that part of the cortex which is internal to the fifth layer of Campbell-layer of small stellate cells) that is, that the hippocampal formation passes directly to the nucleus amygdalae. The amygdaloid nucleus has its own fibre tracts, such, for instance, as the stria terminalis (taenia semicircularis), which does not pass into one of the many rays of white matter, as many of the different tracts of the cortex do, but goes its own way.

LITERATURE

ANTHONY, R. "La morphologie du cerveau chez les singes et chez l'homme." *Revue Anthropologique*, 1917.

ANTHONY ET SANTA MARIA. "Le territoire central du néopallium chez les Primates." *Revue Anthropologique*, 1912.

BRODMANN, K. "Feinere Anatomie des Grosshirns." In Lewandowsky's *Handbuch der Neurologie*, vol. I. 1910.

CAMPBELL, A. *Histological studies on the localisation of cerebral function*, 1905.

DÉJERINE, M. ET MME. *Anatomie du système nerveux*, vols. I and II. Paris, 1895–1901.

ELLIOT SMITH, G. "On some problems relating to the evolution of brain." Arris and Gale Lectures. *Lancet*, 1910.

ELLIOT SMITH, G. "The Central Nervous System" in Cunningham's *Text-book of Anatomy*. Fourth edit. 1917.

GRAY, H. *Anatomy descriptive and applied*. Eighteenth edit. 1913.

HOLL, M. "Ueber die Insel des Carnivorenhirns." *Arch. f. Anat. und Physiol.* 1899.

—— "Ueber die Insel des Ungulatenhirns." *Arch. f. Anat. und Physiol.* 1900.

—— "Ueber die Insel des Menschen und Anthropoiden Gehirs." *Arch. f. Anat. und Physiol.* 1902.

ARIËNS KAPPERS, C. "The Phylogenesis of the Palaeo- and Archicortex compared with the progressive evolution of the Visual Neo-cortex." *Arch. of Neurology*, vol. IV. 1908.

LANDAU, E. "Quelques considérations sur le corps godronné." *Compt. Rend. d. Séances de la Soc. de Biologie de Paris*, T. LXXIX. 1916.

—— "Die Vorderhirnganglien." *Arch. Suisse de Neurologie et de Psychiatrie*, vol. III. 1918.

LUYS. *Atlas photographique du système nerveux*, 1888.

MONAKOW, C. V. *Gehirnpathologie*, vol. I. second ed. 1905.

OBERSTEINER, H. *Anleitung beim Studium des Baues der nervösen Zentralorgane*, fifth ed. 1912.

VOELSCH, M. "Zur vergleichenden Anatomie des Mandelkerns und seiner Nachbargebilde." Part I and II *Arch. for mikrosk. Anat.* vol. LXVIII and LXXVI (1906 and 1910–11).

VRIES, H. DE. "Bemerkungen zur Ontogenie und vergleichenden Anatomie des Claustrums." *Folia Neurobiologica*, vol. IV. 1910.

WILDER, BURT. G. "Brain," in the *Reference Hand-book of the Medical Sciences*, 1902.

A NOTE ON PROFESSOR LANDAU'S MEMOIR ON "THE COMPARATIVE ANATOMY OF THE NUCLEUS AMYGDALAE, THE CLAUSTRUM AND THE INSULAR CORTEX"

By G. ELLIOT SMITH

In transmitting the manuscript of his memoir for publication in the *Journal* Professor Landau courteously invited me to rectify any inaccuracies in his statement of my views. I have thought it the better course to leave his statement of the case as he wrote it and add this comment. One of his sentences I have altered: he had stated that Professor Anthony and I had adopted Holl's theory in a modified form, whereas my interpretation was framed quite independently of Holl's work and before Holl's memoirs were published: Professor Anthony accepted my views and not Holl's. In the *Transactions of the Linnean Society* (Second Series—Zoology, vol. VIII. 1902, especially p. 409) I have discussed this matter at some length, and explained the differences between Holl's interpretation and mine. A brief statement of my conclusions was published in this *Journal* (vol. XXXVI. 1902, p. 309), and the preliminary studies that led me to these results are found in the Catalogue of the Museum of the Royal College of Surgeons published in the same year.

In the first mentioned of these three memoirs I explained in detail my reasons for regarding the suprasylvian sulcus of Carnivores as homologous "partly with the superior limiting sulcus [of the insula] and partly with the upper (or posterior) part of the Sylvian fissure of Lemurs and Apes" (p. 409), whereas Holl attributed to the ectosylvian sulcus the rôle which I assigned to the suprasylvian. My chief reasons for not making these corrections in Professor Landau's memoir were, in the first place, the fact that he does not seem to be acquainted with my earlier writings, and, secondly, because most of the reasons he has given (as evidence against the view that the insular area in Primates corresponds to the anterior limb of the lowermost arcuate gyrus of such a brain as the cat's) have been used by me as arguments in favour of this interpretation (see my Linnean memoir, p. 410). Although this was written long before the histological localisation had been determined, I see no reason for modifying the essential part of my suggested homology.

Elsewhere in the present number of the *Journal* I have discussed the genesis of the claustrum and nucleus amygdalae and explained how it has happened that these two structures are cortical in origin but are not simply delaminations of the deepest layer of the cortex.

My new proposals are based upon the observation that in foetal and primitive adult brains the claustrum is the upturned continuation of the pallium at the ventral edge of the area piriformis and lies partly (or in some cases wholly) under cover of the piriform cortex. It is clear also that the extent of the claustrum can afford no certain or reliable indication of the homologies of the neopallial area that happens to be related to its lateral surface.

Much of the contradiction, which Professor Landau has so clearly brought out in his memoir, is explained by the facts just mentioned. Incidentally they dispose of his criticism of Obersteiner's view (p. 356) that the nucleus amygdalae contains "cellular elements similar to those in the cerebral cortex." The nucleus amygdalae is probably a composite body consisting of a nucleus of hypopallium, together with both hypopallial and palaeostriatal elements derived from the nucleus caudatus and nucleus lentiformis.

ON THE HOMOLOGIES OF THE AUDITORY OSSICLES AND THE CHORDA TYMPANI

By EDWARD PHELPS ALLIS, Jr,

Menton, France

In a work still in press (Allis, 1919), but of which the general summary has just been published (Allis, 1918), I came to the conclusion that the cavum tympanicum of mammals was represented, in fishes, in the pars jugularis of the trigemino-facialis chamber, a diverticulum of the spiracular canal, or an independent evagination of the pharynx, having expanded into that part of that chamber of fishes and so formed the middle ear of mammals. It was assumed that the lateral wall of this chamber of fishes had been broken through in connection with the formation of the external meatus and the tympanic membrane, and that portions of the wall had been utilized to form the auditory ossicles, and possibly also the annulus tympanicus. The chorda tympani, which traverses the cavum tympanicum of mammals, would then necessarily have traversed the trigemino-facialis chamber of fishes, and hence be a pretrematic nerve.

In a later work, also still in press (Allis, 1918), I described two rows of cartilaginous branchial rays found one along the anterior and the other along the posterior edge of each of the branchial arches of Polypterus. The partially fused bases of the dorsal rays of each of these two rows were said to form imperfect bars of cartilage which projected dorso-mesially at a considerable angle to the epal and pharyngeal elements of the arch, and, passing lateral to the vena jugularis, were attached to the cranium, dorsal to that vein, by connective tissues. In the hyal arch, these basal bars of the branchial rays actually reached the cranium, dorsal to the jugular vein, and, having later there acquired articular relations with it, became the prefacialis and postfacialis portions of the teleostean hyomandibula. Either the epihyal alone, or the coalesced and greatly reduced epihyal and pharyngohyal, then became the interhyal of current descriptions. The symplectic was said to probably be a portion of the anterior branchial-ray bar of the hyal arch that lay ventral to, and continuous with, the part of that bar that had been utilized to form the prefacialis portion of the hyomandibula. In the mandibular arch, the basal bars of these two rows of branchial rays became the ascending and otic processes of the palatoquadrate of amphibians, and hence the epipterygoid and the otic process of the quadrate of reptiles, and the pedicel of the alisphenoid and the lateral wall of the trigemino-facialis chamber of fishes.

This view of the origin of these several skeletal structures from branchial rays is simply a modification and further development of the one proposed by me in an earlier work (Allis, 1915), but it is much more fertile in suggestions, and, led by these suggestions to reconsider the chorda tympani, I have come to certain conclusions regarding it, the tympanic cavity and the auditory ossicles that differ from those set forth in the published summary of the first one of the two unpublished works above referred to. These conclusions are accordingly here briefly presented, without any reference to the extensive literature of the subject excepting only to a recent work by Goodrich, and to one of Drüner's several works.

In early embryos of Lacerta, the dorsal end of the blastema of the hyal arch is said by Goodrich (1915) to pass inward between the vena capitis lateralis (vena jugularis) above and the arteria carotis interna below. This blastema later acquires a sharp bend, and separates, at that bend, into dorsal and ventral portions, the dorsal, columellar portion having a horizontal position, and the ventral, cornual portion a vertical one. The columellar portion then develops into a stout rod of cartilage, which has a mesial, stapedial portion which fits into the fenestra ovalis, and a lateral, extracolumellar portion which is applied to that region of the body-wall that will later become the middle portion of the tympanic membrane. About midway on the columella two processes develop, one dorsal and the other antero-internal, both of these processes, as shown in the figures given, lying lateral to the vena capitis lateralis and the arteria carotis interna. The dorsal process has a swollen dorsal extremity which later separates off from the columella and, as the intercalary, becomes fixed to the parotic portion of the cranium. The antero-internal process projects towards the quadrate, and later becomes attached to it by ligament. The nervus facialis runs outward ventral to the vena capitis lateralis, and sends its ramus palatinus ventrally and forward dorso-anterior to the columella. The truncus hyomandibularis facialis runs posteriorly dorsal to the columella and then outward posterior to the dorsal process of that cartilage, and there gives off its chorda tympani branch, which runs forward lateral to both processes of the columella and then internal to Meckel's cartilage. The terminal portion of the chorda thus lies postero-internal to the quadrate as well as to Meckel's cartilage, and ventro-postero-internal to the antero-internal process of the columella, for that process is connected with the quadrate by ligament.

The stapedial portion of the columella of Lacerta thus has the relations to the vena capitis lateralis, the arteria carotis interna, and the nervus facialis that the pharyngeal element of each branchial arch of fishes always has to those same vessels and the nerve of its arch (Allis, 1915), and hence is quite certainly the pharyngohyal. The dorsal process of the columella has the relations to the truncus hyomandibularis facialis and the vena capitis lateralis that the anterior articular head of the hyomandibula of fishes has, and hence, like that head of the hyomandibula, has been derived from the

anterior row of branchial rays of the hyal arch. The extracolumella would seem to represent the epihyal. The antero-internal process of the columella has the relations to the nerves and blood vessels that the symplectic of fishes has, and hence probably represents that element. The chorda tympani of Lacerta is thus certainly the homologue of the ramus mandibularis internus facialis of fishes, and hence, as Goodrich states, a posttrematic nerve. Its serial homologue in each of the branchial arches of fishes is that branch of the posttrematic nerve of that arch that is said by Stannius (1849) to be distributed to the anterior surface of the arch, but which, in Amia (Allis, 1897) and Menidia (Herrick, 1899), is continued onward onto the internal surface of the ceratobranchial of the arch. This branch may accordingly be called the ramus posttrematicus internus of the nerve of the arch.

The mandibular blastema of Lacerta is said by Goodrich to give rise to the quadrate and Meckel's cartilage, but it evidently must also give rise to the epipterygoid, if, as is currently considered to be the case, that structure forms part of the mandibular arch. Both the quadrate and the epipterygoid lie lateral to the vena capitis lateralis and the arteria carotis interna, the quadrate projecting upward and acquiring articular relations with the parotic region of the cranium, the intercalary being wedged in between the two cartilages at this point. The nervus trigeminus runs outward between the quadrate and the epipterygoid, the epipterygoid and the otic process of the quadrate thus being formed, respectively, by the basal bars of the anterior and posterior rows of branchial rays of the mandibular arch. The quadrate articulates with Meckel's cartilage, and hence contains the epal element of the mandibular arch, here fused with the basal bar of the posterior row of branchial rays; the quadrate of Lacerta thus corresponding to the quadrate of fishes plus the lateral wall of the trigemino-facialis chamber, and the epipterygoid corresponding to the pedicel of the alisphenoid.

In embryos of the chick, Goodrich says that the conditions differ from those in Lacerta in that the chorda tympani runs forward internal, and hence anterior, to the dorsal process of the columella, and anterior also to the spiracular cleft. This relation of this nerve to the dorsal process of the columella does not necessarily imply that it is a pretrematic one, for in Polypterus the ramus mandibularis internus facialis, which is unquestionably a ramus posttrematicus internus, runs outward anterior to the anterior articular head of the hyomandibula. In this fish this nerve has, however, probably not, as might be assumed, cut through the basal bar of the anterior row of branchial rays, from its posterior to its anterior surface. It has simply slipped over onto the anterior (lateral) surface of the hyal arch by passing forward beneath the ventral end of that part of the anterior branchial-ray bar that was utilized to form part of the hyomandibula; this apparently being related to the marked reduction of the symplectic in this fish. This change in position of this nerve does not, however, change the relations of the nerve to the spiracular cleft, and if the relations of the chorda of the chick to that cleft are as described by

Goodrich, they are, in my opinion, conclusive evidence that that nerve is a pretrematic one, for I can see no warrant whatever for assuming that a nerve could, as a result of some secondary modification of related parts, change its typical relations to a gill cleft. The chorda tympani of the chick, as identified and described by Goodrich, is thus probably a ramus pretrematicus internus facialis, but it is to be noted that there is, in Goodrich's figures and descriptions of this vertebrate, no indication of a ramus posttrematicus internus facialis.

Goodrich says that the stapes of Trichosurus is derived from the dorsal end of the hyal blastema, and that it chondrifies separately around the stapedial artery. Drüner (1904) says that the stapes of the mouse is derived from the mandibular blastema. It lies ventral to the vena capitis lateralis, thus being the pharyngeal element of whichever arch it may belong to, and as it is shown by Drüner lying postero-ventral to the large superficial petrosal nerve (ramus palatinus facialis), it would seem as if it must be the pharyngeal element of the hyal arch, and not that element of the mandibular arch, for the pharyngeal nerves of fishes never, so far as I know, run forward dorsal to the pharyngeal element of the next anterior arch, this certainly being true of the pharyngeal branch of the nervus glossopharyngeus in Polypterus, Amia, Scomber and the Mail-cheeked fishes. That part of the hyal blastema of Trichosurus that lies ventral to the stapes and dorsal to the cornu is said by Goodrich to grow upward lateral to the vena capitis lateralis and the arteria carotis interna, and to form the lateral hyoid (stylohyal), or intercalary. The truncus hyomandibularis facialis runs posteriorly dorsal to the stapes and internal to the lateral hyoid, and then turns outward posterior to the latter cartilage, between it and the mastoid process. The lateral hyoid thus corresponds to the dorsal process of the columella of reptiles, and hence to the anterior articular head of the hyomandibula of fishes, and that part of the hyal bar to which it is immediately related must be the epihyal. The mastoid process corresponds, in its relations to the truncus hyomandibularis facialis and the vena capitis lateralis, to the posterior articular head of the hyomandibula of fishes.

The truncus hyomandibularis facialis, having issued between the lateral hyoid and the mastoid process, through the stylomastoid foramen, there gives off its chorda tympani branch, which runs forward lateral to the lateral hyoid, and hence is, as Goodrich states, a posttrematic nerve and quite unquestionably the homologue of the chorda of Lacerta. It is shown by Drüner (1904, fig. 10) running forward ventral to the stapes, which would be the normal relations of a ramus posttrematicus internus facialis to the pharyngeal element of the mandibular arch, but not to that element of the hyal arch. The relations shown by Drüner could however have been readily acquired even if the stapes were the pharyngeal element of the hyal arch, for, if that element of the arch were to become detached from the epal element and acquire attachment to some element of the mandibular arch, the ramus posttre-

maticus internus facialis would pass interno-ventral to it, the stapes thus actually lying dorsal to the nerve.

The incus and malleus of Trichosurus are said by Goodrich to both be derived from the dorsal end of the mandibular blastema, the malleus nevertheless being said to represent the dorsal, articular portion of Meckel's cartilage, which latter cartilage actually belongs to the ventral half of the mandibular bar. The incus is said to develop, dorsal to the malleus, as an independent cartilage, and it lies lateral to the vena capitis lateralis and the arteria carotis interna, lateral and hence anterior to the nervus facialis, and posterior to the nervus trigeminus. The incus thus has to these nerves, and to the artery and vein, the relations that the basal bar of the posterior row of mandibular branchial rays of fishes must have had, and those rays of fishes were primarily independent of the branchial bar of their arch, but in articular relations with it. The malleus, with which the incus articulates, must then be the epal element of the mandibular arch, and the independent development of the incus, and its articulation with the malleus, are both primary relations and normally accounted for. The dorsal, process-like end of the incus, which forms the crus breve incudis, is said by Drüner to be in contact with the otic capsule dorsal to the vena petrosa lateralis (vena capitis lateralis), and the incus articulates ventrally with the malleus. Its ventro-posterior corner is prolonged into a process, the crus longum incudis, and a mesial process of this crus is said to be primarily in contact with the otic capsule but to later become separated from it. The distal end of the crus is, according to Drüner, always in articular contact with the lateral end of the stapes, the stapes being considered by him to be developed from the mandibular blastema. The basal bar of the posterior row of mandibular rays would then here simply have acquired contact with both the epal and pharyngeal elements of its arch, which is wholly normal. According to Goodrich, the articular contact of the stapes and incus is secondarily acquired, the stapes being derived by him from the hyal blastema. Under this interpretation of the conditions the basal bar of the posterior row of mandibular branchial rays has acquired articular contact both with the epal element of its own arch, and the pharyngeal element of the hyal arch, this last articulation recalling the articulation, found in the Selachii, of the extrabranchial of an arch with the pharyngeal element of the next posterior arch. The malleus is thus, in either case, the epal element of the mandibular arch, and its later separation from the remainder of the bar of the arch is simply the normal segmentation between the epal and ceratal elements of the arch.

The processus pterygoideus has the relations to the nerves and blood vessels of the pharyngeal element of either the mandibular or the premandibular arch, and would be the one or the other according as the stapes is derived from the hyal or the mandibular arch. In fishes it apparently forms the prepalatinus portion of the floor of the trigemino-facialis chamber.

If the homologies above proposed are correct, as they would seem to be,

the cavum tympanicum of mammals is something more than the trigemino-facialis chamber of fishes, for the stapes, which apparently represents the postpalatinus portion of the floor of the latter chamber, lies considerably dorsal to the floor of the cavum tympanicum. This is also in accord with Drüner's statement that, in the mouse, the space that lies internal to the incus, between the dorsal end of the crus breve incudis above, and the ventral end of the crus longum incudis and the stapes below, is an antrum petrosum laterale similar to the one described by him in Salamandra; for this antrum of the mouse lies definitely dorsal to the two pockets of the tympanic cavity that lead toward the future tympanic membrane, and I have shown (Allis, 1914) that the antrum of Salamandra is the homologue of the trigemino-facialis chamber of fishes. Furthermore, Goodrich says that these two pockets of the tympanic cavity are parts of a secondarily developed diverticulum of the spiracular cleft which projects outward ventral to the chorda tympani, and that the tympanic membrane develops in relation to its lateral wall. This diverticulum would thus necessarily lie external to the trigemino-facialis chamber, and the chorda would traverse it, and not, as I formerly concluded (Allis, 1919), that part of the cavum tympanicum that is represented in the trigemino-facialis chamber.

The tympanic membrane is said to lie ventro-posterior to Meckel's cartilage, and hence, as would naturally be expected, between the hyal and mandibular arches. In fishes, the region of the future tympanic membrane must then lie postero-ventral to the quadrate, and quite certainly postero-ventral also to the posterior process of the teleostean quadrate. The symplectic of the adult teleost lies between this posterior process and the body of the quadrate, but this relation to the quadrate must be a secondary one if the symplectic is derived, as I have suggested (Allis, 1918), from a portion of the anterior branchial-ray bar of the hyal arch. If that be its derivation, it is evident that, as the ventral portion of the spiracular cleft became closed and separated from the ectoderm in the manner described by Goodrich, and as the hyo-mandibula assumed the position inclined to the remainder of the hyal bar that it actually has in the adult teleost, that part of the hyal branchial-ray bar that represents the symplectic would project ventro-anteriorly across the external surface of the ventral portion of the spiracular cleft, and, being elastic, would be capable of vibratory movement. This then doubtless led to the development of the tympanic membrane at this point, and the symplectic was naturally enclosed within it. The symplectic then lost its primary connection with the hyal bar, and became attached to the quadrate as the manubrium mallei.

The quadrate of fishes thus having been utilised, in whole or in part, to form the malleus of mammals, it is evident that the articulation, of the part so utilized, with Meckel's cartilage must have been previously replaced by some other articulation. In the Selachii, Meckel's cartilage articulates with the quadrate by two contiguous articular surfaces, the mesial one of which is

by a condylar process of the quadrate with a facet on Meckel's cartilage, and the lateral one by a facet on the quadrate with a condylar process of Meckel's cartilage (Gegenbaur, 1872, p. 192). In Amia these two articulations are also found, the lateral one being by a condylar process at the ventral end of the coronoid process of Meckel's cartilage with a facet, lined with cartilage, on the distal end of the fused symplectic and posterior process of the quadrate (Allis, 1897). The preoperculum is here closely applied to the external surface of the fused symplectic and posterior process of the quadrate, and the dermarticular and supra-angular are similarly applied to the external surface of the coronoid process; these dermal bones thus adding greatly to the solidity of the joint. In most, if not all of the Teleostei, the posterior process of the quadrate is also found, but it is here a part of the quadrate and gives support to the ventral end of the preoperculum. In Lepidosteus it is found as an independent bone which is in articular contact with a projecting portion of the articular head of the quadrate (Allis, 1909, pp. 63–4). The conditions in Amia and Lepidosteus would accordingly seem to indicate that this process of the quadrate was not primarily a part of that bone, and it may perhaps have been derived either from the mandibular branchiostegal or branchial rays. In any event, the lateral one of the two well developed articulations of Amia presents certain marked advantages over the mesial one, and if it alone were to be retained, the body of the quadrate would be left free for other use. Furthermore, the dentary, which is intimately related to the lateral one of these two articulations, bears the teeth of the lower jaw, and this bone of fishes certainly represents the most important component of the inferior maxillary bone of mammals. There thus seems every reason to justify the conclusion that it is the lateral one of the two articulations of Amia that has become the definitive articulation of mammals, the quadrate of that fish then being freed to be utilized to form one of the chain of auditory ossicles. Whether the dermarticular fused with the dentary, and so became part of the inferior maxillary bone of mammals, as Drüner concludes, or was utilized to form the os tympanicum, as many authors conclude, would not affect the homologies proposed, and there would not have been, at any time, any discontinuity in the articulation of the mandible, or any radical change in that articulation, both of which are acknowledged to be serious objections to Reichert's theory.

PALAIS DE CARNOLÈS,
MENTON, FRANCE.
October 14th, 1918.

LITERATURE

ALLIS, E. P. JR. (1897). "The Cranial Muscles and Cranial and First Spinal Nerves in Amia calva." *Journ. Morphol.* vol. XII.

—— (1909). *The Cranial Anatomy of the Mail-cheeked Fishes, Zoologica*, Bd. XXII. (Hft. 57).

—— (1914). "The Trigemino-facialis Chamber in Amphibians and Reptiles." *Anat. Anz.* Bd. 47.

—— (1915). "The Homologies of the Hyomandibula of the Gnathostome Fishes." *Journ. Morphol.* vol. XXVI.

—— (1918). "The Myodome and Trigemino-facialis Chamber of Fishes and the Corresponding Cavities in Higher Vertebrates." (Preliminary communication.) *Proc. Nat. Acad. of Sciences, U.S.A.* vol. IV.

—— (1919). *Ibid.* In Press.

—— (1918). *On the Origin of the Hyomandibula of the Teleostomi.* In Press.

DRÜNER, L. (1904). "Ueber die Anatomie und Entwickelungsgeschichte des Mittelohres beim Menschen und bei der Maus." *Anat. Anz.* Bd. XXIV.

GEGENBAUR, C. (1872). *Das Kopfskelet der Selachier. Untersuchungen zur Vergleichenden Anatomie der Wirbeltiere.* Hft. 3, Leipzig.

GOODRICH, E. S. (1915). "The Chorda Tympani and Middle Ear in Reptiles, Birds, and Mammals." *Q.J.M.S.* vol. LXI.

HERRICK, C. J. (1899). "The Cranial and First Spinal Nerves of Menidia: a Contribution upon the Nerve Components of the bony fishes." *Journ. Comp. Neurol.* vol. IX.

STANNIUS, H. (1849). *Das peripherische Nervensystem der Fische.* Rostock.

A VARIATION IN THE DISTRIBUTION OF THE RADIAL BRANCH OF THE MUSCULO-SPIRAL NERVE

By J. R. LEARMONTH,

Student of Medicine, University of Glasgow

The anomalous distribution of the radial nerve to be described is of interest on account of its rarity. It forms a marked exception to the general statement of Stopford (*Jour. of Anat.*, LIII. Pt. I, October, 1918), that "this nerve rarely appears to supply the extensive area of skin usually supposed." It seems worthy to be recorded both on this account and because of its possible clinical significance. The case occurred in the Dissecting Room of the University of Glasgow.

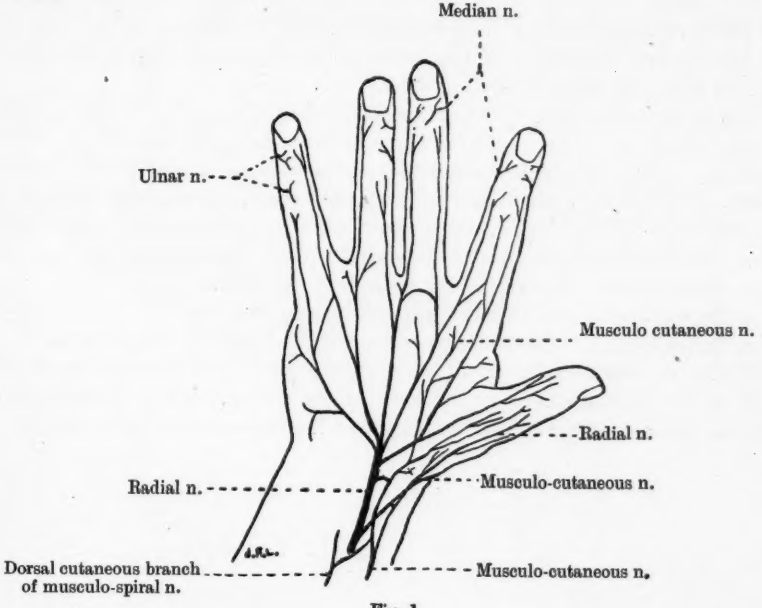


Fig. 1.

In this instance the dorsal branch of the ulnar nerve is entirely absent, and the cutaneous filaments for the medial part of the dorsum of the hand and the dorsal digital branches for the fourth and fifth fingers are branches

of the radial. The radial nerve reaches the dorsum of the hand in the usual manner, and, having given a branch to the lateral side of the thumb, divides immediately distal to the carpal joint into five branches, which are distributed as follows (fig. 1):

The first divides to supply the ulnar side of the thumb as far as the terminal phalanx and the radial side of the index finger as far as the base of the second phalanx.

The second and third divide into digital branches for the adjacent sides of the index and third fingers and third and fourth fingers, respectively, as far as the bases of the second phalanges. The palmar digital branches of the median are distributed as usual to the dorsum of the terminal phalanges.

The fourth divides to supply the adjacent sides of the fourth and fifth fingers, but these branches, unlike the others, reach the terminal phalanges and displace the twigs from the palmar digital branches of the ulnar nerve.

The fifth supplies the ulnar border of the fifth finger as far as the end of the second phalanx, and also gives filaments to the ulnar side of the dorsum of the hand. The ulnar border of the terminal phalanx of the fifth finger is supplied by dorsal branches of the palmar digital branch of the ulnar nerve.

The radial nerve has, therefore, extended postaxially to replace almost completely the ulnar nerve, but preaxial to it the musculo-cutaneous nerve has entered into the supply of the thumb and index finger, and so invaded the area normally supplied by the radial.

The posterior division of the cutaneous branch of the musculo-cutaneous nerve communicates freely with the trunk of the radial nerve and ends in two branches; a lateral, which reaches the metacarpo-phalangeal joint of the thumb, and a medial, which accompanies the branch of the radial nerve to the radial side of the index finger. Both branches communicate with the corresponding digital branches of the radial nerve. The anterior division of the musculo-cutaneous nerve is distributed to the dorsum of the thumb as far as the metacarpo-phalangeal joint, and gives a large branch of communication to the branch of the radial nerve to the lateral side of the thumb.

The lower cutaneous branch of the musculo-spiral nerve (dorsal cutaneous nerve of the forearm) ends at the level of the carpal joint by joining the posterior division of the cutaneous branch of the musculo-cutaneous nerve.

INDEX

Alisphenoids of the Sauropsida, homologies of, Edward Phelps Allis, Jr, 209
Allis, Edward Phelps, Jr, on the homologies of the auditory ossicles and the chorda tympani, 363
— the homologies of the Alisphenoids of the Sauropsida, 209
Amphibia and reptiles, the pterygoids and parasphenoid in, H. Leighton Kesteven, D.Sc., M.B., Ch.M., Syd., 223
— notes on, D. M. S. Watson, M.Sc., 239
Anal canal, stenosis of, note on a case of defective development of the diaphragm accompanied by, Miss O. G. Fisk and Miss O. G. Potter, 26
Anomalies, arterial, of the human leg and foot, an interpretation of the recorded, H. D. Senior, M.D., F.R.C.S., 130
Arterial anomalies of the human leg and foot, an interpretation of the recorded, H. D. Senior, M.D., F.R.C.S., 130
Auditory ossicles and the chorda tympani, homologies of, Edward Phelps Allis, Jr, 363

Bladder, urinary, capacity of, and pressure of fluid in, Ralph Thompson, Ch.M., F.R.C.S., 241
Buchanan, Gwynneth, D.Sc. (Melb.), and Elizabeth A. Fraser, D.Sc. (Lond.), the development of the urogenital system in the marsupialia, with special reference to *Trichosurus vulpecula*. Part I. Edited with an introductory note by Prof. J. P. Hill, D.Sc., F.R.S., 35
— Part II, Elizabeth A. Fraser, D.Sc. (Lond.), 97

Chorda tympani and the auditory ossicles, homologies of, Edward Phelps Allis, Jr, 363
Claustrum, nucleus amygdalae, and the insular cortex, comparative anatomy of, Prof. E. Landau, M.D., 351
— note on, G. Elliot Smith, 361
Corpus striatum, preliminary note on the morphology of, and the origin of the neopallium, G. Elliot Smith, F.R.S., 271
Cranium, primordial, of *Miniopterus schreibersi* at the 17 millimetre total length stage, Professor Fawcett, M.D., 315
Cutaneous nerves of the hand and digits, variation in distribution of, John S. B. Stopford, M.D., 14

Diaphragm, defective development of, accompanied by stenosis of the anal canal, Miss O. G. Fisk and Miss O. G. Potter, 26
Digits and hand, cutaneous nerves of, variation in distribution, John S. B. Stopford, M.D., 14
Duodenal curve, formation of, J. Ernest Frazer, F.R.C.S., 292

Fawcett, Professor, M.D., the primordial cranium of *Miniopterus schreibersi* at the 17 millimetre total length stage, 315
Fisk, Miss O. G., and Miss O. G. Potter, note on a case of defective development of the diaphragm, accompanied by stenosis of the anal canal, 26
Fluid, pressure of, in the urinary bladder, Ralph Thompson, Ch.M., F.R.C.S., 241
Foetus, human, abnormal ribs and vertebrae in, C. L. Pasricha, B.A. (communicated by W. L. H. Duckworth), 254
Foot and leg, human, an interpretation of the recorded arterial anomalies of, H. D. Senior, M.D., F.R.C.S., 130
Fraser, Elizabeth A., D.Sc. (Lond.), and Gwynneth Buchanan, D.Sc. (Melb.), the development of the urogenital system in the marsupialia, with special reference to *Trichosurus vulpecula*. Part I. Edited with an introductory note by Prof. J. P. Hill, D.Sc., F.R.S., 35
— Part II, Elizabeth A. Fraser, D.Sc. (Lond.), 97
Frazer, J. Ernest, F.R.C.S., the formation of the duodenal curve, 292

Gastro-intestinal tract of the Hindus, some observatiohs on, Dr N. Pan, 259
Goodrich, Edwin S., F.R.S., Note on the reptilian heart, 298
— on the development of the pericardiaco-peritoneal canals in Selachians, 1

Hand and digits, cutaneous nerves of, variation in distribution, John S. B. Stopford, M.D., 14
Heart, reptilian, note on, Edwin S. Goodrich, 298
Hill, Prof. J. P., D.Sc., F.R.S.; *see* Gwynneth Buchanan, D.Sc. (Melb.) and Elizabeth A. Fraser, D.Sc. (Lond.)
Hindus, gastro-intestinal tract of, some observations on, Dr N. Pan, 259
Homologies of the alisphenoids of the sauropsida, Edward Phelps Allis, Jr, 209
— of the auditory ossicles and the chorda tympani, Edward Phelps Allis, Jr, 363

Insular cortex, nucleus amygdalae and the claustrum, comparative anatomy of, Prof. E. Landau, M.D., 351
— note on, G. Elliot Smith, 361

Kesteven, H. Leighton, D.Sc., M.B., Ch.M., Syd., the pterygoids in amphibia and reptiles and the parasphenoid, 223

Landau, Prof. E., M.D., the comparative anatomy of the nucleus amygdalae, the claustrum and the insular cortex, 351
Learmonth, J. R., a variation in the distribution of the radial branch of the musculospiral nerve, 371
Leg and foot, human, an interpretation of the recorded arterial anomalies of, H. D. Senior, M.D., F.R.C.S., 130

Marsupialia, development of the urogenital

system in, with special reference to *Trichosurus vulpecula*. Part I. Gwynneth Buchanan, D.Sc. (Melb.) and Elizabeth A. Fraser, D.Sc. (Lond.). Edited with an introductory note by Prof. J. P. Hill, D.Sc., F.R.S., 35
— Part II, Elizabeth A. Fraser, D.Sc. (Lond.), 97
Maturation of the human ovum, Arthur Thomson, 172
Meatus, male urinary, Ralph Thompson, Ch.M., F.R.C.S., 32
Miniopterus schreibersi, primordial cranium of, at the 17 millimetre total length stage, Professor Fawcett, M.D., 315
Musculo-spiral nerve, a variation in the distribution of the radial branch of, J. R. Learmonth, 371

Neopallium, origin of, preliminary note on the morphology of the corpus striatum and, G. Elliot Smith, F.R.S., 271
Nerve, musculo-spiral, a variation in the distribution of the radial branch of, J. R. Learmonth, 371
Nerves, cutaneous, of the hand and digits, variation in distribution of, John S. B. Stopford, M.D., 14
Nucleus amygdalae, the claustrum and the insular cortex, comparative anatomy of, Prof. E. Landau, M.D., 351
— note on, G. Elliot Smith, 361

Obituary notice of A. M. Paterson, M.D. (Edin.), F.R.C.S. (Eng.), Lieut-Col. R.A.M.C., 266
Ovum, human, maturation of, Arthur Thomson, 172

Pan, Dr N., some observations on the gastro-intestinal tract of the Hindus, 259
Parasphenoid and the pterygoids in amphibia and reptiles, H. Leighton Kesteven, D.Sc., M.B., Ch.M., Syd., 223
— notes on, D. M. S. Watson, M.Sc., 239
Pasricha, C. L., B.A., abnormal ribs and vertebrae in a human foetus (communicated by W. L. H. Duckworth), 254
Paterson, A. M., M.D. (Edin.), F.R.C.S. (Eng.), Lieut-Col. R.A.M.C., Obituary Notice, 266
Pericardiaco-peritoneal canals in Selachians, development of, Edwin S. Goodrich, F.R.S., 1
Peritoneal-pericardiaco canals in Selachians, development of, Edwin S. Goodrich, F.R.S., 1
Potter, Miss O. G., and Miss O. G. Fisk, note on a case of defective development of the diaphragm, accompanied by stenosis of the anal canal, 26
Pterygoids and the parasphenoid in amphibia and reptiles, H. Leighton Kesteven, D.Sc., M.B., Ch.M., Syd., 223
— notes on, D. M. S. Watson, M.Sc., 239
Pulmonary lobe, accessory, of the vena azygos, E. Philip Stibbe, 305

Reptiles and amphibia, the pterygoids and parasphenoid in, H. Leighton Kesteven, D.Sc., M.B., Ch.M., Syd., 223
— notes on, D. M. S. Watson, M.Sc., 239
Reptilian heart, note on, Edwin S. Goodrich, F.R.S., 298
Ribs and vertebrae, abnormal, in a human foetus, C. L. Pasricha, B.A. (communicated by W. L. H. Duckworth), 254

Sauropsida, homologies of the alisphenoids of, Edward Phelps Allis, Jr, 209
Selachians, development of the pericardiaco-peritoneal canals in, Edwin S. Goodrich, F.R.S., 1
Senior, H. D., M.D., F.R.C.S., an interpretation of the recorded arterial anomalies of the human leg and foot, 130
Smith, G. Elliot, F.R.S., a preliminary note on the morphology of the corpus striatum and the origin of the neopallium, 271
— a note on Professor Landau's memoir on "the comparative anatomy of the nucleus amygdalae, the claustrum and the insular cortex," 361
Stenosis of the anal canal, note on a case of defective development of the diaphragm accompanied by, Miss O. G. Fisk and Miss O. G. Potter, 26
Stibbe, E. Philip, the accessory pulmonary lobe of the vena azygos, 305
Stopford, John S. B., M.D., the variation in distribution of the cutaneous nerves of the hand and digits, 14

Thompson, Ralph, Ch.M., F.R.C.S., the capacity of, and the pressure of fluid in, the urinary bladder, 241
— the male urinary meatus, 32
Thomson, Arthur, the maturation of the human ovum, 172
Trichosurus vulpecula, development of the urogenital system in the marsupialia, with special reference to. Part I. Gwynneth Buchanan, D.Sc. (Melb.) and Elizabeth A. Fraser, D.Sc. (Lond.). Edited with an introductory note by J. P. Hill, D.Sc., F.R.S., 35
— Part II, Elizabeth A. Fraser, D.Sc. (Lond.), 97

Urinary meatus, male, Ralph Thompson, Ch.M., F.R.C.S., 32
Urogenital system in the marsupialia, development of, with special reference to *Trichosurus vulpecula*. Part I. Gwynneth Buchanan, D.Sc. (Melb.) and Elizabeth A. Fraser, D.Sc. (Lond.). Edited with an introductory note by Prof. J. P. Hill, D.Sc., F.R.S., 35
— Part II, Elizabeth A. Fraser, D.Sc. (Lond.), 97

Vena azygos, accessory pulmonary lobe of, E. Philip Stibbe, 305
Vertebrae and ribs, abnormal, in a human foetus, C. L. Pasricha, B.A. (communicated by W. L. H. Duckworth), 254

Watson, D. M. S., M.Sc., notes on Mr Kesteven's paper on the pterygoids in amphibia and reptiles and the parasphenoid, 239

CAMBRIDGE: PRINTED BY J. B. PEACE, M.A., AT THE UNIVERSITY PRESS

Cambridge University Press

THE VERTEBRATE SKELETON.

By S. H. Reynolds, M.A., Professor of Geology in the University of Bristol. Second edition. Demy 8vo. 17s. net. Cambridge Zoological Series.

MORPHOLOGY AND ANTHROPOLOGY. A Handbook for Students.

By W. L. H. Duckworth, M.A., M.D., Sc.D., University Lecturer in Physical Anthropology. Second edition. Demy 8vo. Vol. I. 12s. net. (To be completed in four volumes.)

GROWTH IN LENGTH: EMBRYOLOGICAL ESSAYS.

By Richard Assheton, M.A., Sc.D., F.R.S., Trinity College, Cambridge. Demy 8vo. With 42 illustrations. 2s. 6d. net.

LECTURES ON THE HISTORY OF PHYSIOLOGY during the Sixteenth, Seventeenth and Eighteenth Centuries.

By Sir M. Foster, K.C.B., M.D., D.C.L. Demy 8vo. With a frontispiece. 10s. net.

POST-MORTEM METHODS.

By J. Martin Beattie, M.A., M.D. Professor of Bacteriology, University of Liverpool. Demy 8vo. With 8 plates and 3 text figures. 12s. net. Cambridge Public Health Series.

WAR NEUROSES.

By John T. MacCurdy, M.D., Psychiatric Institute, Ward's Island, New York; Lecturer on Medical Psychology, Cornell University Medical School, New York. With a Preface by W. H. R. Rivers, M.D., (Lond.). Demy 8vo. 7s. 6d. net. Cambridge Medical Series.

CEREBRO-SPINAL FEVER.

By Michael Foster, M.A., M.D., Captain Royal Army Medical Corps, Territorial Force, and J. F. Gaskell, M.A., M.D., Captain Royal Army Medical Corps, Territorial Force. Large royal 8vo. With 11 plates (6 in colour), 5 charts, and 3 text-figures. 12s. 6d. net.

INSTINCT IN MAN. A Contribution to the Psychology of Education.

By James Drever, M.A., B.Sc., D.Phil., Lecturer on Education in the University of Edinburgh. Demy 8vo. 9s. net.

THE PSYCHOLOGY OF SOUND.

By Henry J. Watt, M.A., Ph.D., D.Phil., Lecturer on Psychology in the University of Glasgow. Royal 8vo. 10s. 6d. net.

AN INTRODUCTION TO THE STUDY OF COLOUR VISION.

By J. Herbert Parsons, D.Sc., F.R.C.S., Ophthalmic Surgeon, University College Hospital. Roy. 8vo. With coloured frontispiece and 75 text figures. 12s. 6d. net. Cambridge Psychological Library.

Fetter Lane, London, E.C. 4
C. F. Clay, Manager